

Reproduction and Social Regulation of Sexual Maturation
in Relation to Population Cyclicity in Bank Voles,
Clethrionomys glareolus

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Title and subtitle Reproduction and social regulation of sexual maturation in relation to population cyclicity in bank voles, <i>Clethrionomys glareolus</i> .		
Abstract Reproduction in bank voles, <i>Clethrionomys glareolus</i>, from two populations, one in North Sweden (NS) and one in South Sweden (SS) was studied. The NS population was strongly cyclic, whereas the SS one was noncyclic. In NS, reproduction was dependent on the phase of the cycle and was markedly suppressed during the peak years. In particular, the sexual maturation of young of the year was inhibited. The SS animals showed no differences in litter size or rate of sexual maturation between years. The reproductive season was longer and the litter size lower in SS. When held in captivity, the reproduction of NS and SS animals was qualitatively similar. The litter size was smaller for primiparous than for multiparous females, and survival of young was maximal in litters 2 to 4. Young from medium to small litters showed better survival and they also grew faster. Females had a post-partumestrus, and because of a lactational delay of implantation, post-partum pregnancies were a few days longer than the normal 18 days. Despite the qualitative similarities, there were quantitative differences, similar to those seen in the field. NS animals were larger and had larger litters, and their young grew faster. The social environment had a marked influence on sexual maturation in males. In SS males, presence of known adults of either sex during the puberty period had little effect on maturation, but daily confrontations with unknown animals caused a marked suppression of maturation. The sex or age of the unknown animals was of little importance; a suppression was caused by adult males, adult females, and juvenile males. NS males appeared to be much more sensitive to social suppression of maturation. NS males, grown up in groups of four were markedly suppressed compared to isolated, while no effect whatsoever was seen in group-reared SS males. The differences between NS and SS animals are consistent with the hypothesis that selection favours a higher reproductive rate in cyclic than in noncyclic populations. The experiments on sexual maturation indicate that the rate of migration is very important in determining the number of young of the year, showing social suppression. The fact that even juvenile animals could cause a suppression of maturation suggests that the total number of animals present in a population rather than the number of adults is important in density dependent suppression of reproduction. High population density is uncommon in SS but common in NS. Therefore, the selective pressure for developing density dependent suppression of reproduction may be higher in NS than in SS. This may explain the greater sensitivity of NS animals to social suppression.		
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REPRODUCTION AND SOCIAL REGULATION OF SEXUAL MATURATION IN
RELATION TO POPULATION CYCLICITY IN BANK VOLES,
CLETHRIONOMYS GLAREOLUS.

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1.0 LIST OF PAPERS

This thesis is based on the following papers, which will be referred to by their Roman numerals.

- I. Gustafsson, T.O., 1983. Reproduction and demography in one cyclic and one noncyclic population of bank vole, *Clethrionomys glareolus*. Manuscript.
- II. Gustafsson, T., Andersson, C.B. and Westlin, L. 1980. Reproduction in a laboratory colony of bank vole, *Clethrionomys glareolus*. Can. J. Zool. 58:1016-1021.
- III. Gustafsson, T.O., Andersson, C.B. and Westlin, L.M. 1983. Reproduction in laboratory colonies of bank vole, *Clethrionomys glareolus*, originating from populations with different degrees of cyclicity. Oikos 40 (In press).
- IV. Gustafsson, T.O. 1983. Influence of the social environment on sexual maturation of male bank voles, *Clethrionomys glareolus*. Manuscript.
- V. Gustafsson, T.O. and Andersson, C.B. 1980. Social environment and sexual maturation in male bank voles, *Clethrionomys glareolus* (Schreber, 1980). Säugetierk. Mitt. 28:310-312.
- VI. Gustafsson, T.O., Andersson, C.B. and Nyholm, N.E.I. 1983. Comparison of sensitivity to social suppression of sexual maturation in captive male bank voles, *Clethrionomys glareolus*, originating from populations with different degrees of cyclicity. Oikos 41 (In press).



2.0 INTRODUCTION.

The bank vole, Clethrionomys glareolus, has a wide distribution, occurring in almost all of Europe, and in a few isolates in South Siberia as far east as Lake Baykal (Corbet, 1978). The population dynamics of bank vole populations differ markedly in different parts of this area. Populations in northern Europe are strongly cyclic, whereas those in western Europe, including Denmark and South Sweden are more or less stable (Wiger, 1979; Hansson, 1979; Jensen, 1982).

In cyclic populations, many reproductive parameters are different in different parts of the cycle. High density years almost universally show a shortening of the breeding season, a lowering of the incidence of breeding, and a suppression of maturation of young. Another common change is a decrease in litter size during peak years (Schaffer and Tamarin, 1973). The body weight of adults generally increase with increasing population density (Chitty, 1952). Virtually all young born during May - June in low density years, but few if any in peak years, reach maturity and breed during the summer of birth. Thus, the amount of suppression is probably the most important factor in determining the total reproductive output in a cyclic population.

In noncyclic populations, much less variation between years in reproduction is seen (Nyholm and Meurling, 1979).

Apart from the lack of variation between years in noncyclic populations, there appears to be marked overall differences in reproduction between cyclic and stable populations of Microtines. Stenseth (1978) and Stenseth and Framstad (1980) suggest that selection favours different reproductive adaptations in cyclic and stable populations. A higher rate of reproduction is favoured in cyclic than in noncyclic populations. A comparison of reproductive rates in cyclic and noncyclic Microtus agrestis and Clethrionomys glareolus provide evidence for this hypothesis (Stenseth, Hansson and Ugland, 1983). The occurrence of cyclic and stable populations of the same species in Scandinavia gives very good opportunities to study basic differences between cyclic and noncyclic populations.

The aims of my work were:

1. To compare reproduction in bank voles from cyclic and noncyclic populations. Such comparisons are useful in detecting fundamental differences between cyclic and noncyclic populations.
2. To detect density dependent regulation of reproduction in such populations.
3. To clarify which factors in an animal's social environment are important in density dependent suppression of reproduction. This work was concentrated on sexual maturation, since this appears to be the most important variable.

3.0 RESULTS.

3.1 Field Study (Paper I).

The sites chosen for the study were Ammarnäs in North Sweden and Revinge in South Sweden. In North Sweden, the bank vole population was markedly cyclic. The eight year study period covered more than two cycles. The fluctuations were violent, the estimated density during the largest peak was more than 400 times that during the lowest period. In South Sweden, the population was noncyclic, and neither very high nor very low densities were met with.

The reproductive and demographic changes during the population cycle in North Sweden were similar to those seen in other cyclic populations. As the population density increased, fewer young of the year reproduced. This resulted in a successively lower proportion of the young being born in the second half of the breeding season, and a successive increase in the mean age of the overwintered individuals. The litter size was maximal in increase years, decreased somewhat during the peak and was lowest during the decline.

In South Sweden, no density dependent differences in reproduction could be detected. Late autumn - winter breeding was seen in some years, and this resulted in large differences in age structure between years. Winterbreeding in noncyclic populations appears to be correlated with high production of tree seeds (Jensen, 1982).

On the average, the breeding season was longer, and the litter size was lower in the noncyclic than in the cyclic population.

3.2 Reproduction In Captivity (Papers II And III).

Animals from the North and South Swedish populations were used as founders for laboratory colonies, and the reproduction in the colonies was compared.

Qualitatively, the reproductive biology of animals from the cyclic and the noncyclic population were similar (II, III). Primiparous females had smaller litters than multiparous ones. Survival of young was dependent on parity and litter size. Maximal survival was seen in the second through fourth litter, whereas first litter and litters after the fourth showed less survival. Survival was best in small to medium sized North Swedish, and medium sized South Swedish litters. Young from small to medium sized litters also grew faster than young from large litters.

The duration of pregnancy was 18 days for nonlactating females. Females normally showed postpartum estrus, and in lactating females, the pregnancy was prolonged in proportion to the number of sucklings. This prolongation is caused by a delay in implantation (Andersson and Gustafsson, 1979).

Despite the qualitative similarities, there were marked quantitative differences (III). The North Swedish animals were larger, had larger litters, and their young grew more rapidly. The intervals

between births were slightly longer in North Swedish than in South Swedish females. A much higher mortality of young seen in North Swedish animals was probably a laboratory artifact.

3.3 The Social Environment And Sexual Maturation Of Males (IV, V, VI).

Presence of adult animals of either sex during the postweaning period had little effect on the maturation of South Swedish males (IV). Presence of an adult female caused a slight suppression of maturation, whereas no effect at all was seen of presence of an adult male.

In contrast, daily confrontations with unknown animals caused a marked suppression of maturation of males (IV, V). This effect was not sex or age dependent, a suppression was seen after confrontations with adult males, adult females, or juvenile males. Laboratory mouse females had no effect, however, indicating some degree of species specificity. It is unclear if physical contact is necessary for the suppression, in any case exposure to bedding, soiled by unknown males had no effect.

North Swedish males appear to be more sensitive to social suppression of maturation than South Swedish ones (VI). When compared to isolated males, North Swedish males which had grown up in groups of four showed a marked suppression of maturation. No such effect was seen in South Swedish males.

4.0 CONCLUSIONS.

The thesis does not help in explaining the reasons for population cyclicity, but it points out very marked differences in reproduction between cyclic and noncyclic populations. The differences, since they are seen also in laboratory populations, appear to be genetic. They are consistent with Stenseth's (1978) hypothesis that different reproductive rates are selected for in cyclic and stable populations. Geographic variation in reproductive rate has been explained in other ways. Innes (1978) and others suggest that a shift towards older and more fecund females in more northern populations cause larger litter size. The data presented in this thesis are not consistent with such a hypothesis. Genetic differences in litter size were seen (III) and fecundity was independent of age in the laboratory work (II). In the field work, no correlation was seen between age structure and litter size (I).

A selection for larger litter sizes in areas with shorter breeding season as suggested by Spencer and Steinhoff (1968) seems consistent with the data in paper I, but the estimates of the length of the breeding season are uncertain. Stenseth, Hansson and Ugland (1983) found very small differences in the length of the breeding season between North Sweden and South Sweden in both Microtus agrestis and Clethrionomys glareolus.

The higher sensitivity to social suppression of maturation seen in cyclic than in noncyclic animals is interpreted in the following way: At high population density, selection favours animals which show a suppression of maturation.

Possible advantages are:

1. The animals avoid aggression from mature animals.
2. An inhibition of maturation is accompanied by a cessation or slow down of body growth. If the population peak is followed by a winter with food scarcity, a smaller animal with less food demands may have a higher probability of survival.

Densities high enough to favour evolution of density dependent regulation of maturation occur regularly in cyclic populations, and there is strong selection for such mechanisms. In noncyclic populations, such high densities are seldom seen, and density dependent mechanisms have a low selective value.

The inhibition caused by confrontations with unknown animals show that South Swedish animals do have some density dependent suppression of maturation. These experiments indicate that the amount of migration in the population is a very important factor in determining the degree of suppression of maturation. Stenseth (1983) has compiled data showing that the rate of dispersal increases with increasing cyclicity. This may lead to larger differences in the amount of suppression between cyclic and noncyclic populations than would be expected from density alone.

As this work shows that even immature animals can cause suppression of reproduction in other animals, another implication is that the early cessation of breeding seen at high population densities may be caused by that the mature animals are suppressed by contacts with large numbers of immature animals.

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REPRODUCTION AND DEMOGRAPHY IN ONE CYCLIC AND
ONE NONCYCLIC POPULATION OF BANK VOLE,
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ABSTRACT

Population dynamics and reproduction was studied in two populations of bank voles, Clethrionomys glareolus, one in North Sweden and one in South Sweden. The North Swedish population was followed for eight, and the South Swedish for six years.

The South Swedish population showed irregular, noncyclic fluctuations in population density, whereas the North Swedish one was cyclic, with three minima and two maxima during the study period.

There were marked reproductive differences between the populations. The over all litter size was larger in the cyclic than in the noncyclic population. The breeding seasons were long in South Sweden, and winter breeding was seen in several winters. Differences in the amount of late autumn breeding led to large, irregular shifts in the age structure of overwintered individuals. In North Sweden, differences between seasons were related to density. At low density, most of recruitment was from the late summer cohort, but at high density the spring cohort dominated. This led to a successive increase in the age of overwintered animals during the cycle, with maximal age during the crash year.

The noncyclic population showed no differences in reproduction between years, and a high proportion of the young of the year reached maturity in all years. In the cyclic population, most of the parameters studied were dependent on the phase. Body weight increased with increasing density, and the litter size was maximal in the increase years, intermediate during peaks and minimal during crash and low-density years.

Probably the most important factor in density dependent regulation of reproduction was the rate of sexual maturation of young of the year. The proportion of young reaching maturity in the cyclic population was inversely related to density, with an almost total suppression during one of the peaks.

1.0 INTRODUCTION

The bank vole, Clethrionomys glareolus, is a species which exhibit multiannual cycles in density in parts of its range of distribution but is noncyclic in other parts. Cyclic populations are found in most of Fennoscandia whereas populations in South Sweden and most of western Europe are noncyclic (Hansson, 1979; Jensen, 1982; Myllymäki, Christiansen and Hansson, 1977). Microtus agrestis appears to show a similar pattern, at least in Scandinavia (Myllymäki, Christiansen and Hansson, 1977).

Reproductive characteristics of animals from cyclic and noncyclic populations are likely to be subjected to very different selective pressures. Stenseth and Framstad (1980) suggested that selection should favour larger litter size and a more rapid sexual maturation in cyclic populations than in noncyclic ones. The idea that there are genetic differences in reproduction between cyclic and noncyclic populations finds support in a laboratory study. Gustafsson, Andersson and Westlin (1983) found marked differences in reproduction in agreement with those predicted by Stenseth and Framstad (1980) between Clethrionomys glareolus from a cyclic and a noncyclic population when kept in a constant laboratory environment. The occurrence of both stable and markedly cyclic populations of the same species means an unique opportunity to study effects of different selective pressure in areas with different population dynamics.

Stenseth, Hansson and Ugland (1983) found marked reproductive differences between cyclic and noncyclic populations of Microtus agrestis and Clethrionomys glareolus. Breeding seasons were shorter and litter sizes were larger in the cyclic populations. Using proportions of pregnant females they found that during the increase phase, and for overwintered females, more young were born per female per day in the cyclic than in the noncyclic population. For young of the year females, the opposite was true. In both species, the reproductive season was shorter in the peak than in the increase year. The results were interpreted as evidence for genetic differences between the populations. Using partly the same data as the previous authors, Nyholm and Meurling (1979) reported marked differences in reproduction between cyclic and noncyclic populations of Clethrionomys glareolus. In the noncyclic population, no differences between years in litter size or rate of sexual maturation were seen, whereas large differences between years in both litter size and rate of sexual maturation were seen in the cyclic. There were also indications that young from the cyclic population could reach sexual maturity at a lower age than those from the noncyclic population.

The present study is an extension of that by Nyholm and Meurling (1979). It includes most of the material presented there, and extends the study period to from 5 to 6 years for the noncyclic and from 3 to 8 years for the cyclic population. The aim was to describe reproductive and demographic differences between cyclic and stable populations.

2.0 MATERIAL AND METHODS

2.1 Sampling

Bank voles, *Clethrionomys glareolus*, were collected in 2 areas, Stensoffa and Björnstorp, in Skåne, South Sweden (56°N , 14°E), and in one area, Ammarnäs, in Swedish Lapland (66°N , 16°E). Snap traps baited with dried apple and cotton wick, soaked in vegetable oil and wheat flour, were used. Except for 1976 - 1978 in South Sweden, the trapping method used was the Small Quadrat method (Myllymäki, Paasikallio, Pankakoski and Kanervo, 1971). Traps were set in 15×15 m squares, with 3 traps in each corner, squares were at least 100 m apart. Traps were usually set for four nights, sometimes only for two nights.

A total of 1149 bank voles were trapped in two areas in South Sweden, approximately 15 km apart. The main biotopes used were beech forest and reforestations at Stensoffa and reforestations at Björnstorp. The study period was from early summer 1972 to late winter 1978, in the Björnstorp area only from autumn 1972 to autumn 1975. No differences between animals from these two localities were seen and the animals were combined. Trapping was performed at all times of the year. In South Sweden the Small Quadrat method described above was used only during 1972 to 1975. After 1975, nonrandom trapping methods were used. Thus, no density estimates for South Sweden during 1976 - 1978 are available. During 1972 - 1975, bank voles were trapped in collaboration with Dr. L. Hansson, Swedish University of Agricultural Sciences.

In Ammarnäs, North Sweden, 1248 bank voles were trapped during 1975 - 1982. The biotopes trapped were mature spruce and pine forests and mature birch forest just above the range of the conifers. Trapping was mainly performed in June to August, in 1976 - 78 and 1980 - 81, a September sample was also made. Winter samples (January to April) were only collected in 1978.

2.2 Animal Treatment

Animals were weighed and sexed. Reproductive organs were dissected out, weighed fresh and fixed in Bouin's fluid. In females, the numbers of embryos, corpora lutea and placental scars were noted as also presence and number of resorbing embryos. Ovaries from approximately one third of the pregnant animals were routinely processed for histology, and macroscopic corpora lutea counts were checked by microscope examination.

In males, in addition to gonad weight, the condition of the testicles, healthy-looking or regressing, was noted.

2.3 Age Estimation

The first lower molar was used for age estimation (Pucek and Zedja, 1968). In laboratory material, the modal age at which the two roots separate was approximately 2 months (Gustafsson, Andersson and Westlin, 1982). After the separation of the roots, the growth rate was assumed to be 0.15 mm/month. Birth dates were calculated from the age estimates. The frequency distribution of birth dates were used as

estimates of the breeding season. There are some problems: It is likely that the individual variation in growth rate is considerable, in laboratory bred animals, Gustafsson, Andersson and Westlin (1982) found that the 90 per cent confidence interval for an animal of an estimated age of 6 months was approximately ± 2 months. There may also be a bias in the age estimates. No measurements of actual growth rate of the molar roots has been made in any of these populations. Thus, this method can not be used for estimating the beginning and end of the breeding season; the relative length in different years can, however, be compared on the basis of these estimates. Another advantage is that the relative contribution of cohorts born early or late in the seasons to the recruitment can be estimated. Since the method used was similar during the whole study, comparisons between years, and between general patterns in populations, seem justified.

3.0 RESULTS AND DISCUSSION

3.1 Density Variations

Density variations in South Sweden during 1972 - 1975 are described in Hansson (1979) and Myllymäki, Christansen and Hansson (1977).

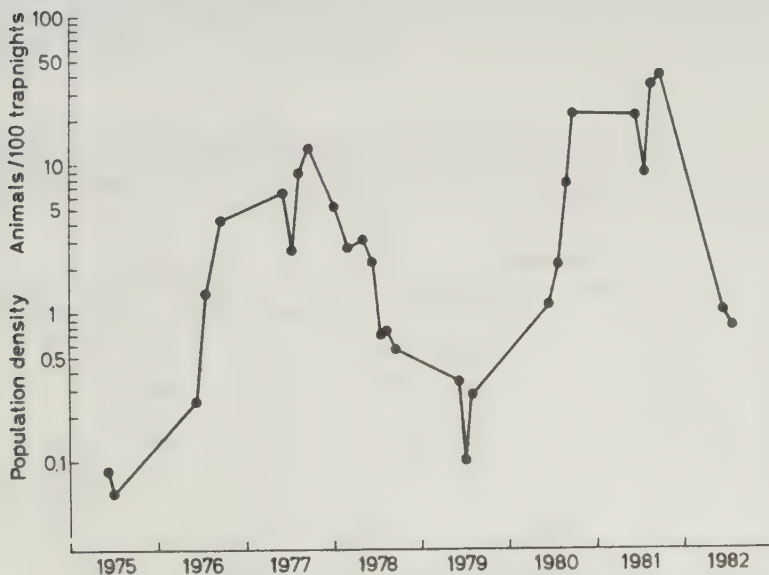


Figure 1. Density of bank voles in North Sweden during the study period.

In summary, there were only seasonal fluctuations in density, and no cyclic pattern in population density was seen. Trapping results in 1976 and 1977 indicate a continuation of the pattern seen in 1972 - 1975. The population in South Sweden appears to be non-cyclic (Hansson, 1979), as is the population of Microtus agrestis in that area (Hansson, 1971).

In North Sweden very marked cyclic fluctuations in population density were seen (Figure 1). The between years variation in population density was much larger than the seasonal variation. Two maxima in density, in 1977 and 1980 - 81, and three minima, in 1975, 1978 - 79, and 1982, were seen. The minimum density was less than 0.1 voles/100 trapnights in 1975 and the maximum was more than 40 in 1981.

3.2 Breeding Season

The length of the breeding season, from the first to the last recorded birth is given in Table 1. This estimate is uncertain, because in many cases very few females were trapped.

In South Sweden, the first litters were born in the middle of May in most years, and the breeding season ended in August - October. Extensive winter breeding was seen in the winter between 1976 and 1977.

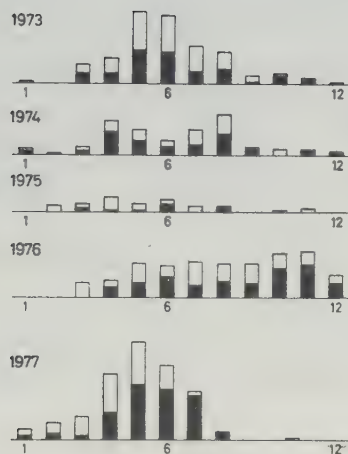
In North Sweden, the sampling started after the initiation of breeding in 1976 and 1977. In 1978, and 1980 - 82, the first litters were born in late May or early June. Breeding ceased in mid August in all years except 1976, when pregnant females were caught in the middle of September.

Table 1. Duration of the breeding season in South and North Sweden. Dates of first and last recorded birth, calculated from captures of pregnant females. Dates within brackets are uncertain due to small sample sizes or no preceeding or following samples that year.

Year	South Sweden		North Sweden	
	First recorded birth	Last recorded birth	First recorded birth	Last recorded birth
1972	(12/5)	(22/8)		
1973	9/5	18/10		
1974	15/5	19/9		
1975	10/5	26/8		
1976	(23/5)	winterbreed.	(20/6)*	15/9
1977	winterbreed.	6/8	(4/6)**	23/8
1978			11/6	(14/8)
1979			(21/6)	(8/8)
1980			1/6	21/8
1981			28/5	17/8
1982			8/6	N.D.

*Three young animals, aged 3, 2 and <2 months were caught in early June.

**Two young (approx. 20 - 25 days old) animals caught in early June.

a**b**

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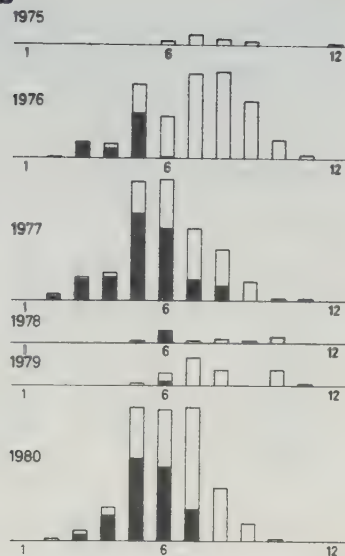


Figure 2. Distribution of estimated birth dates of bank voles from South and North Sweden. Birth dates were calculated from age estimates based on molar roots.

a. South Sweden, b. North Sweden.

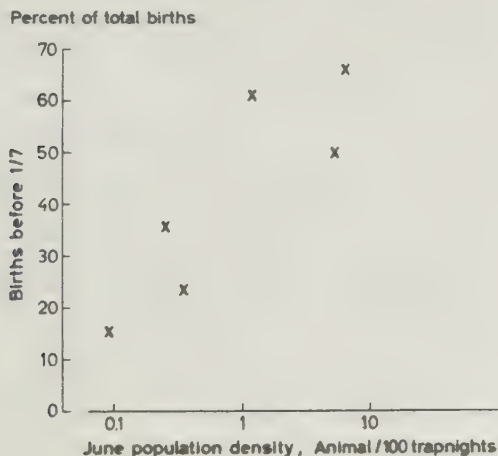


Figure 3. Relation between spring population density and relative contribution of the early summer cohort to recruitment in North Sweden. Animals estimated to have been born before July 1, as per cent of total births for each year.

Table 2. Per cent mature animals (males with testes above 600 mg and females with ovaries above 7 mg) in relation to season in South Sweden during 1972 - 1978. Animals older than 2 months are included. Number of observations given within brackets.

Males

Year/Month	1	2	3	4	5	6	7	8	9	10	11	12
1972					100 (16)		86 (7)			0 (17)	0 (5)	
1973		0 (26)	0 (11)	69 (16)	100 (3)	100 (5)	81 (16)	25 (12)		6 (17)		
1974		0 (26)	0 (5)	100 (10)	100 (8)	86 (7)	100 (6)		25 (8)	77 (13)	0 (2)	
1975	0 (24)	36 (11)	0 (4)	100 (6)	91 (11)	75 (4)		100 (2)		0 (1)	0 (1)	
1976	0 (5)	0 (2)			100 (3)	100 (1)	100 (1)		29 (14)	60 (5)	69 (13)	0 (1)
1977		80 (5)	100 (13)	100 (10)	100 (6)	100 (5)		55 (11)	0 (5)		0 (1)	0 (2)
1978	0 (1)	0 (4)	0 (13)									

Females

Year/Month	1	2	3	4	5	6	7	8	9	10	11	12
1972					100 (10)		100 (2)	100 (1)		0 (8)	0 (7)	
1973		6 (18)	33 (3)	100 (10)	100 (2)	100 (6)	100 (12)	82 (11)		25 (12)		
1974		14 (14)	0 (9)	100 (4)	100 (7)	100 (6)	86 (7)		6 (16)	22 (9)	0 (4)	
1975	14 (21)	42 (12)	33 (3)	100 (5)	100 (7)	100 (5)	0 (1)	50 (2)	0 (1)	0 (2)	0 (2)	
1976	0 (6)	0 (2)			100 (1)	100 (1)	100 (2)		64 (11)	50 (2)	57 (7)	
1977		38 (8)	88 (17)	100 (9)	100 (6)	80 (5)	100 (2)	25 (8)	0 (4)			
1978	0 (3)			0 (2)								

Table 3. Body weight of overwintered female bank voles during the reproductive season in relation to parity. Mean weights, corrected for effect of year of capture and weight of embryos are shown.

	South Sweden		North Sweden	
	N	Body (g)	N	Body (g)
Nulliparous	16	19.0	36	22.8
Primiparous	10	24.1	58	25.8
Multiparous	64	24.2	85	28.4

Statistics: see Table 4.

Table 4. Body weight of overwintered bank voles during the breeding season in different years. Female body weights are corrected for differences due to parity and for weight of embryos.

Year	South Sweden				North Sweden			
	N	Females Body, g	N	Males Body, g	N	Females Body, g	N	Males Body, g
1972	11	24.7	22	24.2				
1973	25	21.4	20	22.9				
1974	19	24.2	22	22.7				
1975	17	24.9	15	22.7			3	20.7
1976	2	25.3	8	21.7	5	24.4	7	20.7
1977	16	22.1	17	22.0	56	27.1	93	26.1
1978					38	22.7	48	22.0
1979					3	20.7	5	17.7
1980					14	26.8	31	24.5
1981					54	29.2	99	27.4
1982					9	24.6	10	24.6

Results of analysis of variance.

South Sweden

Males, Effect of year, $F(5,83) = 1.7$, N.S.

Females, Effect of year, $F(5,76) = 4.7$, $P < 0.01$.

Effect of parity, $F(2,76) = 16.9$, $P < 0.01$.

North Sweden

Males, Effect of year, $F(7,277) = 38.8$, $P < 0.01$.

Females, Effect of year, $F(6,161) = 18.0$, $P < 0.01$.

Effect of parity, $F(2,161) = 35.5$, $P < 0.01$.

Another way to estimate the breeding season is to use the frequency distribution of calculated birth dates as a estimate of the breeding season. The distribution of estimated birth dates for 2 to 15 months old South and North Swedish animals is shown in Figure 2.

The frequency distribution indicate that the breeding season in the North were discrete, with little winter breeding.

The 1976 breeding season appears to have been considerably longer than those of other years. In South Sweden, distribution of births as well as captures of pregnant females indicate longer breeding seasons, and there were signs of breeding in many winters. In one of these winters, 1976 - 1977, this was confirmed by capture of several pregnant females. Many animals caught during the winter 1974 - 1975 showed gonad weights similar to those in summer (Table 2), and although no pregnant or lactating females was caught it is not unlikely that limited breeding took place this winter. No similar signs of gonadal stimulation were seen in any of the other winters, although the birth distribution indicates some winter breeding also during 1973 - 1974.

In the North, the relative contributions of the cohorts to recruitment was density dependent (Figure 3). In years of low density, most animals recruited were estimated to have been born after July 1, whereas in high density years, the major part of recruitment took place before this date. This indicates density dependent differences in either the seasonal pattern of reproduction or the survival of cohorts.

3.3 Body Weight

The body weight of overwintered females was strongly dependent on parity (Table 3). Thus, in order to make comparisons between years, corrections for parity had to be made.

There were no consistent differences in body weight between years in South Sweden (Table 4). Males showed no significant differences at all and although the females showed a significant variation, it was not correlated to the density variations. It must be remembered that density variations were small, however.

In North Sweden, body weight was strongly dependent on population density (Table 4), with highest body weight at highest density. This pattern was clearly seen in both males and females, and is consistent with that observed in most studies of cyclic populations (Krebs and Myers, 1974).

3.4 Age Structure

The age of the overwintered animals varied strongly between years in both populations (Table 5).

In South Sweden, low mean age of the overwintered animals was seen in 1975 and 1977. In 1977, this was preceded by a large amount of late autumn breeding in 1976. In addition to this a number of winter born animals entered the breeding population already in May - June in 1977, which resulted in a very young breeding population that spring. There was no confirmed peak in breeding in the autumn of 1974, which could explain the low age in 1975.

In North Sweden, the mean age of the overwintered animals was related to population fluctuations. The lowest mean age was seen in the year after the crash. From this point, the mean age increased steadily until the next crash (Table 5).

Table 5. Mean age (in months) of overwintered animals during the breeding season (April to September in South Sweden and June to August in North Sweden). Ages are corrected for date of capture.

Year	Mean age of overwintered animals			
	South Sweden N	Age	North Sweden N	Age
1973	(38)	12.8		
1974	(50)	12.5		
1975	(36)	9.9		
1976	(12)	11.8		11.0
1977	(49)	9.3	(146)	11.3
1978			(37)	12.4
1979			(8)	9.7
1980			(29)	11.6
1981			(141)	12.2

Results of analysis of variance.

South Sweden

Effect of year, $F(4,162) = 18.3$, $P < 0.01$.

North Sweden

Effect of year, $F(5,404) = 11.7$, $P < 0.01$.

This pattern, of course, is another reflection of the pattern of birth dates of recruited individuals seen in Figure 3. The change in age structure is consistent with the pattern suggested by Zejda (1967). Wiger (1979) found only small changes in the age of overwintered voles in a cyclic *Clethrionomys glareolus* population in Norway, however.

3.5 Litter Size

Litter size (embryo count) in relation to time of capture, parity and age is given in Table 6.

The overall litter size was much higher in North than in South Sweden (6.35 v.s. 4.87). No significant effects of parity on litter size were seen in either population, nor were there any differences between overwintered females and young of the year. In South Sweden, the litter size was dependent on season, with larger litters in spring than in late summer (Table 8). No such effect was seen in North Sweden.

No difference between years in litter size were seen in South Sweden, but in North Sweden the litter size was correlated to the phase in the population cycle (Table 7). Maximal size was seen in the prepeak years 1976 and 1980, and minimal in the crash - low density years 1978-79 and 1982. The peak years 1977 and 1981 were intermediate. Litter size was correlated with body size, except that the peak years had smaller litter size than that expected from their large body size.

Table 6. Littersize in relation to parity in overwintered and young of the year bank voles from South and North Sweden. The number of observations is given in brackets.

a. South Sweden, overwintered.

	Jan-Apr	May	June	July	August	Sep-Dec
1972						
Primip.		6.0 (3)				
Multip.				3.0 (2)	4.0 (1)	
1973						
Primip.		6.0 (1)				
Multip.			6.0 (4)	11.0 (1)	4.5 (11)	5.0 (1)
1974						
Primip.		6.0 (1)				
Multip.		5.2 (4)	5.7 (3)	3.7 (3)		3.0 (1)
1975						
Primip.		3.5 (2)				
Multip.		6.0 (1)	5.7 (3)			
1976						
Primip.		7.0 (1)				
Multip.						6.0 (1)
1977						
Primip.	4.0 (1)					
Multip.	5.8 (4)	4.5 (2)			4.0 (1)	

b. South Sweden, young of the year.

	Jan-Apr	May	June	July	August	Sep-Dec
1972						
Primip.					3.0 (1)	
Multip.					4.0 (1)	
1973						
Primip.				4.8 (4)	4.0 (2)	3.0 (1)
Multip.						
1974						
Primip.				4.0 (1)		
Multip.				4.5 (2)		
1975						
Primip.					2.0 (1)	
Multip.						
1976						
Primip.				6.0 (1)		4.2 (3)
Multip.						6.0 (3)
1977						
Primip.		5.5 (2)	3.0 (1)		3.0 (1)	
Multip.		6.0 (1)				

c. North Sweden, overwintered.

	Jan-Apr	May	June	July	August	Sep-Dec
1976						
Primip.			5.0 (1)	8.0 (1)		
Multip.				7.3 (3)		
1977						
Primip.			6.0 (10)			
Multip.				6.6 (10)	5.7 (9)	
1978						
Primip.			5.5 (8)			
Multip.					6.0 (2)	
1979						
Primip.			6.0 (1)			
Multip.					5.0 (1)	
1980						
Primip.			8.0 (1)			
Multip.			6.0 (2)	4.5 (2)	9.0 (3)	
1981						
Primip.			6.8 (23)			
Multip.			5.0 (1)	6.2 (10)	6.0 (5)	
1982						
Primip.			5.5 (2)			
Multip.				3.0 (1)		

d. North Sweden, young of the year.

	Jan-Apr	May	June	July	August	Sep-Dec
1976						
Primip.			7.0 (1)	4.7 (3)		
Multip.				8.5 (2)		6.0 (2)
1977						
Primip.				8.0 (1)	5.2 (6)	
Multip.					6.0 (2)	
1978						
Primip.					5.0 (1)	
Multip.						
1979						
Primip.						
Multip.						
1980						
Primip.				6.0 (1)	6.9 (14)	
Multip.					7.9 (7)	
1981						
Primip.					4.0 (1)	
Multip.						
1982						
Primip.						
Multip.						

Table 7. Littersize during the main breeding season of bank voles in different years. Means corrected for age (overwintered or not) and parity are shown.

Year	South Sweden			North Sweden		
	N	Litter-size	Littersize corr. for bodywt.	N	Litter-size	Littersize corr. for bodywt.
1972	6	4.9	4.7			
1973	15	5.1	5.1			
1974	14	4.7	4.7			
1975	7	4.4	4.4			
1976	2	6.7	6.7	11	6.7	7.0
1977	8	4.8	4.8	38	6.0	6.1
1978				11	5.5	6.1
1979				2	5.4	6.4
1980				31	7.2	7.2
1981				40	6.4	6.1
1982				2	4.6	5.0

Results of analysis of variance

Without bodyweight as a covariate.

South Sweden, Effect of year, $F(5,42) = 1.05$, N.S.

North Sweden, Effect of year, $F(6,127) = 2.75$, $P < 0.05$.

With bodyweight as a covariate.

South Sweden, Effect of year, $F(5,42) = 1.05$, N.S.

Effect of bodyweight, $F(1,42) = 3.74$, N.S.

North Sweden, Effect of year, $F(6,124) = 1.94$, N.S.

Effect of bodyweight, $F(1,124) = 10.8$, $P < 0.01$

Table 8. Variation in littersize during the main breeding season in bank voles from South Sweden. Means corrected for age (overwintered or not) and parity are shown.

Month	N	Littersize
May	18	5.5
June	11	5.5
July	11	4.4
August	14	4.0

There was a significant difference between months, $F(3,47) = 3.7$, $P < 0.05$.

The lack of effect of parity on litter size is surprising, since primiparous laboratory bred females from both these areas have clearly smaller litters than multiparous ones (Gustafsson, Andersson and Westlin, 1980, 1983). A spring to autumn decline in litter size could mask an effect of parity on litter size. It may be that both effect of parity and season were present in North Sweden, but that they masked each other. The period between first and last sample in each breeding season was short in North Sweden, resulting in further difficulties in detecting such seasonal trend.

A reduced litter size during the population peak is seen in some cyclic *Microtines*, but not in others (see table in Schaffer and Tamarin, 1973). Nyholm and Meurling (1979) reported a higher litter size in *Clethrionomys glareolus* during an increase year than during two peak years. In *C. rutilus*, Koshkina and Korotkov (1975) found no overall differences in litter size between population phases, but on the average, the litter size decreased more sharply with season in peak years than in low density or increase years.

3.6 Sexual Maturation

In South Sweden, young of the year reached sexual maturity in all years, and many females reproduced in the year of birth (Table 9 a-c). The only time when some tendency towards inhibition of maturation was seen was in 1977, after a winter with extensive breeding. Unfortunately, population density in 1977 is not known, so no correlation can be made.

In North Sweden, the proportion of young reaching maturity or showing gonad stimulation was density dependent. During the years with low to moderate spring density, 1976, 1979 and 1980, almost all young of the year older than 2 months were mature or maturing. During the peak years 1977 and 1981, a much lower proportion reached maturity (Table 9 d-f).

A suppression of sexual maturation of young of the year at high density appears to be a common phenomenon in cyclic *Microtines* (Schaffer and Tamarin, 1972). In *Clethrionomys* species this has been reported for cyclic populations of *C. glareolus* (Wiger, 1979; Nyholm and Meurling, 1979), *C. rufocanus* (Kalela, 1957) and *C. rutilus* (Koshkina and Korotkov, 1975). A similar suppression has also been reported in noncyclic populations of *C. glareolus* (Bujalska, 1975).

4.0 GENERAL DISCUSSION

This paper supports the idea that populations of *Clethrionomys glareolus* are cyclic in North and noncyclic in South Scandinavia (Hansson, 1979; Myllymäki, Christiansen and Hansson, 1977). The reason for the lack of cyclicity in South Sweden is not known. Hansson (1979) suggested that due to lack of a protective snow cover bank voles in South Sweden are very subjected to predation during the winters. This results in a low winter survival. This results in a poor winter survival, and the spring density is reduced to a too low level for a buildup of a population peak. Several authors have emphasized the importance of a good winter survival for cyclicity (Wiger, 1982). Fuller (1967) stated that population cycles are especially characteristic of areas with a good snow cover. In the noncyclic western European populations high production of tree seeds appears to be one of the major causes for winter breeding. (Jensen, 1982). The winter breeding seen in South Sweden in 1976 is probably explained in this way as 1976 was a seed year in Denmark and in a large part of Europe (Jensen, 1982). Unfortunately, it is not known if the winter reproduction in South Sweden in 1976 - 77 was followed by a peak in density.

Table 9. Sexual maturation of young of the year (older and younger than 2 months) in different years. Only the main breeding season is included.

a. South Sweden, per cent young of the year males with testes larger than 200 mg.

Year	Age	May	June	July	August	Total
1973	> 2			57 (7)	44 (9)	50 (16)
	< 2			0 (2)	0 (3)	0 (5)
1974	> 2			100 (2)		100 (2)
	< 2		0 (3)	40 (5)		25 (8)
1975	> 2				100 (2)	100 (2)
	< 2		100 (1)		0 (3)	25 (4)
1976	> 2				71 (7)	71 (7)
	< 2				31 (16)	31 (16)
1977	> 2	100 (1)			10 (10)	18 (11)
	< 2	100 (2)	40 (5)	0 (2)	0 (1)	40 (10)

b. South Sweden, per cent young of the year females perforce.

Year	Age	May	June	July	August	Total
1973	> 2			100 (9)	43 (7)	75 (16)
	< 2		100 (1)	0 (4)	100 (1)	33 (6)
1974	> 2		100 (1)	100 (3)		100 (4)
	< 2		0 (1)	50 (6)		43 (7)
1975	> 2				50 (2)	50 (2)
	< 2		0 (1)	0 (1)	33 (6)	25 (8)
1976	> 2			100 (2)		100 (2)
	< 2					n.d.
1977	> 2	100 (2)	67 (3)	100 (1)	33 (6)	58 (12)
	< 2	100 (2)	0 (4)		20 (5)	27 (11)

c. South Sweden, per cent young of the year females pregnant or with placental scars.

Year	Age	May	June	July	August	Total
1973	> 2			56 (9)	28 (7)	44 (16)
	< 2		0 (1)	0 (4)	0 (1)	0 (6)
1974	> 2		0 (1)	100 (3)		75 (4)
	< 2		0 (1)	17 (6)		14 (7)
1975	> 2				0 (2)	0 (2)
	< 2		0 (1)	0 (1)	17 (6)	12 (8)
1976	> 2			100 (2)		100 (2)
	< 2					N.D.
1977	> 2	100 (2)	67 (3)	100 (1)	33 (6)	58 (12)
	< 2	50 (2)	0 (4)		20 (5)	18 (11)

d. North Sweden, per cent young of the year males with testes larger than 200 mg.

Year	Age	May	June	July	August	Total
1975						N.D.
1976	> 2			95 (20)		95 (20)
	< 2			100 (1)		100 (1)
1977	> 2		100 (1)	100 (3)	50 (16)	60 (20)
	< 2		0 (2)	31 (13)	0 (7)	18 (22)
1978	> 2			0 (1)	100 (1)	50 (2)
	< 2				67 (3)	67 (3)
1979						N.D.
1980	> 2			100 (5)	92 (39)	93 (44)
	< 2			91 (11)	35 (34)	51 (45)
1981	> 2			0 (1)	0 (3)	0 (4)
	< 2			25 (4)	0 (21)	4 (25)

e. North Sweden, per cent young of the year females perforate.

Year	Age	May	June	July	August	Total
1976	> 2		100 (2)	100 (7)		100 (9)
	< 2		100 (1)	100 (1)		100 (2)
1977	> 2				52 (29)	52 (29)
	<			46 (13)	71 (7)	55 (20)
1978	> 2				100 (2)	100 (2)
	< 2					N.D.
1979	> 2				100 (2)	100 (2)
	< 2			0 (1)		0 (1)
1980	> 2			67 (3)	100 (21)	96 (24)
	< 2			60 (5)	57 (21)	58 (26)
1981	> 2				25 (4)	25 (4)
	< 2			0 (2)	0 (35)	0 (37)
1982	> 2					N.D.
	< 2			100 (1)		100 (1)

f. North Sweden, per cent young of the year females pregnant or with placental scars.

Year	Age	May	June	July	August	Total
1976	> 2		50 (2)	86 (7)		78 (9)
	< 2		0 (1)	0 (1)		0 (2)
1977	> 2				45 (29)	45 (29)
	< 2			8 (13)	43 (7)	20 (20)
1978	> 2				50 (2)	50 (2)
	< 2					N.D.
1979	> 2				100 (2)	100 (2)
	< 2			0 (1)		0 (1)
1980	> 2			67 (3)	95 (21)	92 (24)
	< 2			0 (5)	38 (21)	31 (26)
1981	> 2				25 (4)	25 (4)
	< 2			0 (2)	0 (35)	0 (37)
1982	> 2					N.D.
	< 2			0 (1)		0 (1)

Stenseth (1978) and Stenseth and Framstad (1980) discussed the selective pressures operating on reproduction in cyclic and noncyclic populations. They predict that natural selection would favour larger litter size and more rapid sexual maturation in cyclic compared with noncyclic populations. Their model apply to a population where reproduction is not limited by density dependent factors. The very large litter size and very extensive breeding of young of the year in the increase years 1976 and 1978 in North Sweden agree with their prediction. Further, they state that the maximal litter size should be reached earlier in cyclic than in stable populations. This, they interpret as that the ratio between litter size of overwintered and young of the year females should be larger in cyclic populations. Stenseth and Framstad (1980) reported an increase in this ratio with increasing cyclicality in *Clethrionomys rutilus* and Stenseth, Hansson and Ugland (1982) found the same thing in *C. glareolus* and *Microtus agrestis*. The pattern seen in the present study is actually the other way round, a much larger ratio in South than in North Sweden (1.19 and 1.05 respectively when litter sizes are corrected for parity effects and between year differences).

The changes in reproductive parameters and body weight seen during the population cycles in the North Swedish population agrees with those reported for other cyclic populations (Schaffer and Tamarin, 1973). There were clear signs of a density dependent regulation of reproduction. In particular, the sexual maturation of young of the year was suppressed in peak years. This would shift the seasonal maximum in reproduction from late summer during the increase phase to spring during the peak. This is consistent with changes in age structure and estimated distribution of births. Such a shift in reproduction has been reported by for example Wiger (1979) and Zejda (1967).

Innes (1978), Fleming and Rauscher (1978) and Millar (1979) have suggested that geographical gradients in litter size may be caused by a shift towards older and more fecund females when going northwards. The results presented here are not consistent with that hypothesis. The overwintered South Swedish animals are on the whole of similar age as the North Swedish ones. Further, neither the large shifts in mean age of overwintered animals (Table 5) nor the large differences in the number of reproducing young of the year females (Tables 9c,f) result in shifts in litter size in the predicted direction.

One difference between these populations was that there was little evidence of density dependent regulation of reproduction in the South Swedish one. This is contrary to what Bujalska (1973) reported from an stable island population in Poland. In that population maturation of females was dependent on the availability of a home range, and the number reaching maturity was dependent on the number of adult females. However, the population density was very high (Gliwicz, 1975). Possibly, lack of cyclicality may have different causes, an efficient self regulation as in the Polish population, and an external cause, possibly winter predation, keeping the numbers so low that cycles can not develop.

Although no direct evidence is presented here, the results are consistent with the view that selection may lead to differences in reproduction between cyclic and noncyclic populations (Stenseth, 1978). The differences seen agree with those reported for laboratory populations (Gustafsson, Andersson and Westlin, 1983). In particular, the occurrence of high population peaks may lead to that conditions are

more favourable for evolution of density dependent regulation of reproduction in the cyclic than in the noncyclic population. A study by Gustafsson, Andersson and Nyholm (1983) supports this: Male Clethrionomys glareolus from a cyclic population were more sensitive to social suppression of maturation than males from a noncyclic one.

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Reproduction in a laboratory colony of bank vole, *Clethrionomys glareolus*

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Reproduction was studied in a laboratory colony of bank voles, *Clethrionomys glareolus*. Litter size was mainly dependent on parity, the mean being 4.3 in primiparous and 5.3 in multiparous females. Mortality of young during the nursing period was also affected by the order of litter, with a minimum in the third litter (14%). Most of this mortality took place during the first 3 days after birth. Gestation was 18.3 days in primiparous females. Postpartum estrus and mating was usual and the length of the resulting pregnancy was prolonged by lactation (19.1 days for zero sucklings vs. 22 days for four or more sucklings).

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Nous avons étudié la reproduction des campagnols *Clethrionomys glareolus* chez une colonie expérimentale gardée en laboratoire. Le nombre de petits par portée dépend de ce que la femelle est primipare ou non; le nombre moyen de petits est de 4.3 chez une femelle primipare et de 5.3 chez les femelles qui n'en sont pas à leur première portée. La mortalité des jeunes durant la période d'allaitement est également affectée par le rang de la portée; cette mortalité est minimale chez la troisième portée (14%). La mortalité frappe surtout durant les trois premiers jours qui suivent la naissance. Chez les femelles primipares, la gestation dure 18.3 jours. L'ovulation et l'accouplement post partum sont choses communes et la durée de la nouvelle grossesse se trouve prolongée par l'allaitement (19.1 jours lorsqu'il n'y a pas de petit et 22 jours lorsque la femelle nourrit quatre petits ou plus).

[Traduit par le journal]

Introduction

Understanding of population dynamics of small rodents calls for a good knowledge of the reproduction biology of the species concerned. Laboratory studies of reproduction are necessary as such knowledge is difficult to obtain by field studies.

This paper describes reproduction of *Clethrionomys glareolus* in the laboratory. Several laboratory studies have been carried out (Buchalczyk 1970; Drożdż 1963; Mazák 1962; Saint-Girons 1972; Steven 1957; von Wrangel 1940). One of these (Buchalczyk 1970) used a large sample and gave a good description of some aspects of reproduction, but many important aspects were not considered. All others suffer from a small number of observations and nonconstant laboratory environment.

Materials and methods

Data on reproduction and survival of young were recorded in a laboratory colony of bank voles, *Clethrionomys glareolus*, Schreber, 1780, maintained at the Department of Zoology, University of Lund, Sweden. The colony was started with 40 bank voles caught in Skåne, southern Sweden, between autumn 1974 and spring 1975. Of these, 8 females and 11 males took part in breeding. No field animals have been added to the colony since 1975. The data were based on 2844 young in 827 litters from 125 females including the original animals as well as their progeny from the first to the fourth generation.

Voles were kept in monogamous pairs in standard plastic laboratory mouse cages (PAG Presswerk, Essen, Germany), measuring 40 cm × 20 cm × 15 cm, with wire mesh cover, with wood cuttings for bedding and a commercial mouse food (Fors mustfoder, AB Harald Fors & Co., Vadstena, Sweden) and water. Cages were cleaned and carrots were provided twice a week. The animals were kept on a photoperiod of 18 h light and 6 h dark and at a temperature of 22 ± 5°C. Humidity was not regulated. Animals were usually paired when 60 to 180 days old and kept as long as they reproduced successfully. Pairs were killed if the female was not visibly pregnant 50 days after delivery of the preceding litter or after repetitive loss of litters. If the male died while the female still reproduced, a new male was supplied.

Cages with pregnant females were checked daily for litters. Checking included weighing of females, to rule out the possibility of litters being born and eaten without discovery. The day of discovery of young was designated day 0 of lactation and of the succeeding interbirth interval. Records were made of the number of young born and of the numbers of surviving young on days 0-6, day 10, and day 16. The number of young found on day 0 was used as litter size at birth, since it appeared that very few young were completely eaten before discovery. Young were sexed, weighed, and individually marked by toe clipping on day 10 and weaned and weighed on day 16. Young voles were kept in groups of four or five animals of the same sex until pairing.

In part of this study, duration of pregnancy after postpartum mating was determined. To determine the time of mating, vaginal smears were taken once a day, beginning when the young were found. The smear series was continued up to day 4 or 6 of lactation. The smears were taken with a metal probe; they were air dried, heat fixed, stained in Methylene blue, and examined

TABLE 1. Frequency distribution of litter size and percentage of surviving young at weaning in 799 litters of *C. glareolus*

	Litter size									
	1	2	3	4	5	6	7	8	9	10
No. litters	18	44	97	154	211	169	75	22	5	4
% surviving	38.9	60.2	69.4	75.7	81.1	77.9	76.4	74.4	40.0	60.0

for the presence of sperm. The presence or absence of a vaginal plug was noted. The day when sperm or a vaginal plug was found, was designated day 0 of pregnancy.

Results

Litter size

Litter size varied from 1 to 10 with a mode of 5 (Table 1). It was markedly dependent on the sequence of litters (Table 2). For this reason it is not meaningful to give an overall average litter size. As wild females are unlikely to produce more than a few litters and as mean litter size in litters 2–10 was very stable, the laboratory females may for ecological purposes be divided into primiparous ones (mean litter size 4.28 ± 0.13) and multiparous ones including litters 2–10 (mean litter size 5.34 ± 0.06). The difference in mean litter size between these two groups was significant ($T = 6.85$; $P < 0.001$).

Regression analysis was made on litter size versus the age of the female for 230 primiparous females (49 to 324 days old) and on 93 females producing their second litter (70 to 347 days old).

TABLE 2. The number of young per litter and mortality during the suckling period in 791 successive litters of *C. glareolus*

Order of litter	No. of litters	Mean no. in litter ($\pm$ SE)	% mortality
1	104	4.28 ± 0.131	20.2
2	98	5.32 ± 0.140	16.4
3	85	5.36 ± 0.168	14.0
4	70	5.47 ± 0.158	17.2
5	60	5.41 ± 0.180	18.8
6	51	5.39 ± 0.194	23.3
7	46	5.51 ± 0.198	27.8
8	39	5.08 ± 0.228	25.8
9	36	4.86 ± 0.304	30.8
10	34	5.24 ± 0.283	37.7
11	30	4.17 ± 0.304	36.1
12	27	4.26 ± 0.309	34.8
13	24	4.35 ± 0.273	23.3
14	22	4.18 ± 0.299	39.1
15	21	3.35 ± 0.295	47.4
16	17	3.24 ± 0.315	32.7
17	14	3.07 ± 0.305	51.2
18	6	3.20 ± 0.476	37.5
19	4	3.75 ± 0.854	60.0
20	3	2.33 ± 0.667	42.9

No significant correlation was found ($r = -0.037$ and 0.037 respectively).

The mean litter size increased significantly with the number of generations in captivity (Table 3). No seasonal variations in litter size were found.

Mortality of young

Loss of young was much more frequent during the first 2 days after delivery than during the rest of the lactation period (Fig. 1). Seventy percent of the losses took place before the 3rd day. Mortality was influenced by litter size in that young from very small or very large litters showed lower survival than the rest (Table 1).

Order of litter and season also influenced the mortality. In our colony young born from April to June showed higher survival than those born during the rest of the year. The relationship between order of litter and mortality is given in Table 2. Mortality decreased significantly from 20% in the first litter to a minimum of 14% in the third litter (comparison between litters 1 and 3, χ^2 test, $P < 0.025$). After the third litter there was a slight increase in mortality with increasing order of litter.

No consistent effects of generations in captivity or of age of the mothers on mortality of young were found.

Growth of young

Weight of young when 16 days old was negatively correlated with the number of sucklings, except that young from very small litters (one, or for litters with partial survival, two young) were small (Table

TABLE 3. The number of young per litter in 519 litters from wild-caught *C. glareolus* and their offspring in the first to sixth generations

Generations in captivity	no. litters	Mean no. in litter ($\pm$ SE)
Wild caught	48	4.92 ± 0.126
1	75	5.15 ± 0.142
2	103	5.16 ± 0.136
3	98	5.86 ± 0.162
4	71	5.32 ± 0.202
5	82	5.37 ± 0.162
6	42	5.33 ± 0.235

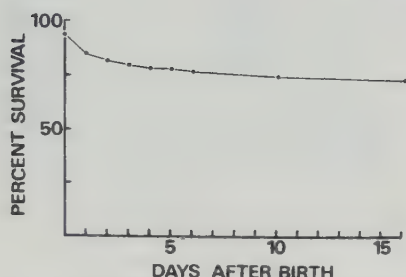


FIG. 1. Survival during the suckling period of 2743 young from 562 litters.

4). Young from litters where all survived until weaning were heavier than those from litters with partial survival (Table 4). The order of litters for a female did not affect the weight of her young. No consistent effects of season or of number of generations in captivity on growth were found.

Pregnancy and interbirth intervals

The duration of pregnancy in 12 primiparous females, from the day of observed mating to the day when young were found in the daily check, was 18.3 ± 0.07 days (mean $\pm$ SE).

The interbirth interval was usually longer than the duration of pregnancy for primiparous females (Fig. 2). In order to determine if postpartum mating was normal, daily vaginal smears were taken from delivery (day 0) for 6 days. Such smear series were taken in 142 cases. In 114 of these a new litter was delivered within 27 days after the previous one. No litters were born between day 28 and 34. Seventeen

TABLE 4. Effect of the number of sucklings on weight of young when 16 days old in 363 litters where all young survived and 201 litters with partial survival

Litters where all young survived			Litters with partial survival		
No. young	N	Weight day 16, g	No. surviving	N	Weight day 16, g
1	6	8.50	1	10	7.00
2	21	9.02	2	30	8.08
3	42	8.94	3	40	8.53
4	73	8.81	4	50	8.30
5	110	8.55	5	41	8.19
6	77	8.24	6	21	8.01
7	29	8.37	7	7	8.75
8	5	6.96	8-9	2	6.62
Total	363		Total	201	
Mean		8.57	Mean		8.20

NOTE: The weight at 16 days was affected by the number of sucklings ($F_{(7, 349)} = 4.66, P < 0.001$) and young in litters with partial survival were smaller than those where all survived ($F_{(1, 349)} = 14.27, P < 0.001$).

cases, where the interbirth interval was 35 days or longer, were excluded. They were assumed to result from matings after the weaning of the previous litter, rather than from postpartum matings. In six of these cases sperm was found postpartum. They probably represent nonfertile matings or resorptions. In the remaining 11 cases no new litters were born. The occurrence of sperm or copulatory plugs in these smear series is given in Table 5. Sperm or a copulatory plug was found in about 60% of the cases. Most of these discovered matings took place very soon after delivery, before the checking when the young were found. A few more matings took place within 2 days after delivery, but no later, ones were seen. The duration of these pregnancies, resulting from the discovered matings, is shown in Fig. 3. It is evident that mating normally takes place soon after delivery and that the cause of the longer interbirth interval for lactating females is not a delayed mating. In view of this, interbirth intervals shorter than 28 days may be regarded as good estimates of postpartum pregnancies. This upper limit was used because the longest recorded pregnancy was 27 days (Fig. 3) and because very few interbirth intervals (13 out of 640) were between 28 and 34 days long. Intervals longer than 34 days were assumed to result from nonpostpartum matings.

The interbirth interval was affected by the number of sucklings. Nonlactating females had shorter interbirth intervals than lactating ones as shown in Fig. 2. The effect of the number of sucklings on the distance to the next litter is shown in Table 6. Only interbirth intervals of 27 days or less were used. The number of young alive on day 5 was used as the number of sucklings because the cause for this prolonged pregnancy is delayed implantation (Andersson and Gustafsson 1979) and because implantation in nonlactating females takes place about day 5. The interbirth interval may be expressed as a function of the number of sucklings: $i = -0.052s^2 + 0.811s + 19.076$, where i = interbirth interval and s = number of sucklings.

Puberty

No attempts to determine the age at puberty were undertaken but the five youngest females to give birth were 27(1), 31(2), 32(4), and 33(4) days old at conception. The three youngest males to sire litters were found by backdating 18 days from birth of the litter to be 34, 37, and 39 days old at mating.

Sex ratio

The sex ratio in litters in which all young survived was 1.12 males to 1 female (1081 to 964) significantly different from 1:1 ($\chi^2 = 6.69, P < 0.001$). When those litters in which some young

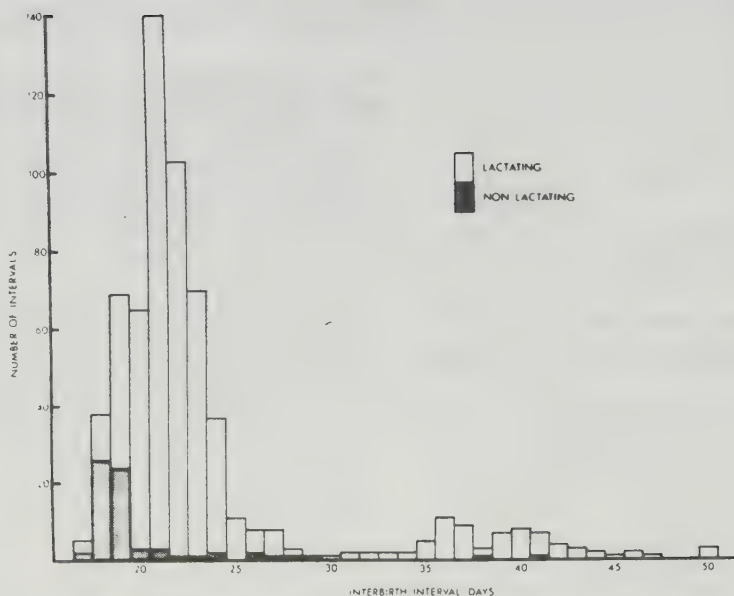


FIG. 2. Distribution of 633 interbirth intervals for lactating ($n = 564$) and nonlactating ($n = 69$) females.

TABLE 5. The occurrence of sperm, or vaginal plugs, in the vaginal smear series of 114 females. The smear series were started immediately postpartum. Only females which delivered a new litter within 27 days are included

	Day postpartum						
	0	1	2	3	4	5	6
No. smears	114	105	103	97	96	63	60
% smears with sperm or copulatory plug	50.9	6.7	1.9	0	0	0	0

died were included the sex ratio was 1.06 males to 1 female (1536 to 1448), which is not significantly different from 1:1. The predominance for males agrees well with other laboratory results (Buchalczyk 1970).

Discussion

Influences of age on reproduction, mortality of young, and intervals between litters are difficult to study in the field. Reproductive characteristics found in laboratory studies may, however, be used with caution in evaluation of field studies.

An influence of age on litter size has been sug-

gested for natural populations of microtines (Stenseth and Framstad 1980). Field observations on bank voles may be taken as evidence for this as yearlings were found to have smaller litters than did overwintered females (Zejda 1966; Nyholm and Meurling 1979). In our opinion, caution is needed when evaluating the factors influencing litter size, as dependence of litter size on age, weight of the female, or parity all will give very similar results. One problem in this study is that females were usually not paired immediately at sexual maturity, whereas in the field, breeding will start at sexual maturation. Nevertheless, our data suggest that

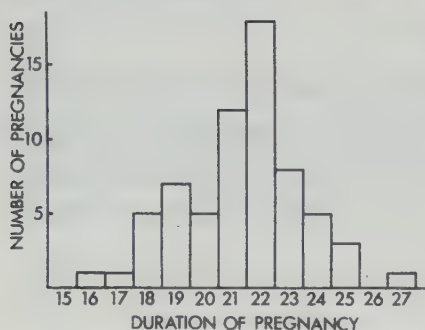


FIG. 3. The duration of 66 pregnancies after postpartum mating. Partly lactating, partly nonlactating females.

litter size is dependent on parity, weight of the female, or population density, rather than age of the female.

In this study primiparous females had smaller litters than multiparous ones did. This agrees well with laboratory findings for other microtines, for example *Microtus arvalis* (Frank 1956), *M. oregoni* (Cowan and Arsenault 1954), *M. ochrogaster* (Richmond and Conaway 1969), *M. montanus* (Negus and Pinter 1965), and *Dicrostonyx groenlandicus* (Hasler and Banks 1975). In contrast to this, Zejda (1966) in a field study of *Clethrionomys glareolus* reported similar litter sizes for primiparous and multiparous females. In *C. rufocanus*, multiparous females had larger litter sizes than primiparous females did (Kalela 1957), although this conclusion was not drawn in the paper.

According to Zejda (1966) heavier females had larger litters than lighter ones did. Unfortunately our weight data were insufficient for estimating the influence of the weight of the females on reproduction. In natural populations litter size is also influenced by population cycles (Nyholm and Meurling 1979).

The effect of generation on litter size was probably due to an involuntary selection for females producing many young.

Field estimates of mortality of young have been made for *Lemmus trimucronatus* (Batzli *et al.* 1974) and for *C. glareolus* (Ryszkowski and Truszkowski 1970). These studies are not comparable with ours because of different methods. Furthermore laboratory estimates of mortality are probably not valid in the field because of the very different conditions. Some relationships may, however, be useful: (1) the more frequent loss of young during the first days after delivery (Fig. 1); (2) the influence of litter size

on mortality (Table 1); (3) the influence of sequence of litters (Table 2). Similarly to our results Buchalczyk (1970) reported higher mortality during the first days after parturition than later and dependency of litter size on mortality.

The influence of the number of sucklings and of mortality on the weight of the young at weaning (Table 4) may be explained in terms of lactational capacity of the females. In small litters young may be expected to get more milk than in large litters and therefore grow faster. The low weight of young from very small litters may be due to insufficient suckling stimulus to maintain enough lactation. The lower weight of young from litters with partial survival may also be explained by lactational capacity of the females. Females with low capacity will produce small young and small young may be susceptible to higher mortality than large young. An alternative explanation would be differences in weight at birth due to litter size. Millar (1975, 1979) has shown that newborn *Peromyscus leucopus* and *P. maniculatus* were lighter in large litters than in small ones.

The duration of pregnancy for primiparous females (18.3 days) agrees well with other findings (von Wrangel 1940; Mazák 1962; Drożdż 1963). From a field study, Coutts and Rowlands (1969) suggested that implantation is delayed in lactating bank voles. This has been confirmed in our laboratory (Andersson and Gustafsson 1979). The high frequency of postpartum matings (Table 5) shows that delayed implantation accounts for most of the prolongation of interbirth intervals (Fig. 2 and Table 6), alone or in combination with a prolonged postimplantation development.

The reason for delayed implantation may be energetic. The energy demands of a pregnant female increase towards the end of pregnancy (Grodzinski and Wunder 1975; Kaczmarek 1966;

TABLE 6. Interbirth intervals for different numbers of sucklings (= number of young alive when 4 days old) in 554 cases. Intervals longer than 27 days are excluded

No. sucklings	No. cases	Time to next litter, days (mean $\pm$ SE)
0	65	19.3 $\pm$ 0.26
1	16	19.0 $\pm$ 0.29
2	38	20.1 $\pm$ 0.24
3	68	21.2 $\pm$ 0.23
4	107	21.5 $\pm$ 0.17
5	128	21.9 $\pm$ 0.14
6	87	22.1 $\pm$ 0.17
7	35	22.3 $\pm$ 0.24
8	8	21.6 $\pm$ 0.42
9	2	22.5 $\pm$ 1.50

Stenseth *et al.* 1980). A lactating female also needs more energy in the later part of lactation (Kaczmarski 1966; Stenseth *et al.* 1980). In *C. glareolus* the lactating period and the pregnancy period are of similar length. If a lactating postpartum pregnant female was to have a pregnancy of "normal" duration, the periods of maximal energy requirements would coincide and furthermore coincide with the time when the female is heaviest and least mobile. A delayed implantation would alleviate this condition.

The small second peak in the frequency distribution of interbirth intervals, between 35 and 41 days (Fig. 2), suggests a lactational anestrus in those females which either did not mate or failed to become pregnant postpartum.

The rapid sexual maturation, with some animals fertile before 40 days of age, agrees well with field studies where young have been found to mature rapidly when they are not inhibited by environmental factors like population density or non-breeding season (Nyholm and Meurling 1979; Zejda 1966).

Acknowledgments

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Reproduction in laboratory colonies of bank vole, *Clethrionomys glareolus*, originating from populations with different degrees of cyclicity

Torgny O. Gustafsson, C. Bertil Andersson and Lilian M. Westlin

Gustafsson, T. O., Andersson, C. B. and Westlin, L. M. 1983. Reproduction in laboratory colonies of bank vole, *Clethrionomys glareolus*, originating from populations with different degrees of cyclicity. – *Oikos* 40: 182–188.

Reproduction in two laboratory colonies of bank vole, *Clethrionomys glareolus* (Schreb.), established with animals from the increase phase of a strongly cyclic population was compared with that in a colony originating from a relatively stable population. Most reproductive variables were influenced by the same factors in the cyclic and non-cyclic animals, but considerable quantitative differences were seen. The cyclic animals were heavier, had larger litters, and faster growth of young. Survival of young was much lower and the intervals between litters were longer in cyclic animals. The results are discussed in relation to reproductive differences between the original populations and in relation to a current hypothesis of evolution of different reproductive rates in populations with different degrees of cyclicity.

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Сравнивали размножение у двух лабораторных колоний полевки *Clethrionomys glareolus* (Schreb.), представленных животными, собранными во время фазы подъема популяции со строгим циклом, с колонией, основанной особями из относительно стабильных популяций. Большая часть репродуктивных переменных определяется одинаковыми факторами у циклических и нециклических популяций, но имеются и значительные количественные различия. Животные из циклических популяций тяжелее, имеют больший помет, с более быстрым ростом молодого поколения. Выживаемость молодых особей гораздо ниже, и интервал между появлением потомства больше у циклических популяций. Обсуждаются результаты исследования репродуктивных различий у исходных популяций и имеющиеся гипотезы возникновения различий в скорости размножения в популяциях с разной степенью циклическости.

1. Introduction

In small rodents many aspects of reproduction may differ between populations of the same species at different locations. For example, litter size has been shown to increase with increasing latitude in *Clethrionomys glareolus* (Schröb.) (Zejda 1966) and in *C. gapperi* (Vigors) (Innes 1978). In addition to this, the population dynamics may be very different in populations at different locations. Populations of field vole (*Microtus agrestis* (L.)) and bank vole (*C. glareolus*) in southern Sweden (55–56°N) show small, irregular annual variations in density. In contrast, populations in northern Sweden show cyclic variations in density with peaks with approximately 3–5 yr intervals (Hansson 1969, Myllymäki et al. 1977, Hörnfeldt 1978, Nyholm and Meurling 1979, Stenseth et al. unpubl.).

In cyclic populations several reproductive variables may vary during the population cycle with markedly depressed reproduction at high densities (Schaffer and Tamarin 1973). Such variables include length of breeding season, rate of sexual maturation, weight at first breeding, litter size, percentage of females breeding and occurrence of winter breeding.

Stenseth (1978) suggested that reproductive variables differ in populations with different degrees of cyclicity because different optimal reproductive rates would be favoured by evolution in stable and unstable populations. Reproductive differences between stable and cyclic populations of *M. agrestis* and *C. glareolus*, in favour of this hypothesis, were presented by Stenseth et al. (unpubl.). Differences in reproduction between North Swedish (cyclic) and South Swedish (stable) populations of *C. glareolus* as well as differences between years in North Swedish populations were also reported by Nyholm and Meurling (1979). These differences could be either genetic or be due to differences in the environment, or both.

The present study aimed at comparing reproduction in colonies of *C. glareolus*, originating from cyclic North Swedish populations with that in a colony from a stable South Swedish population (Gustafsson et al. 1980).

2. Materials and methods

Reproductive data were collected in two laboratory colonies of bank voles kept at the Dept of Zoology, Univ. of Lund, Sweden. Colony A was started with 5 females and 8 males caught in 1976, and colony B with 6 females and 6 males caught in 1977. The animals were collected in Ammarnäs in Swedish Lapland (66°N), and originated from a cyclic bank vole population (Nyholm and Meurling 1979). This population had very low density in 1975 and was in the increase phase in 1976. In the medium to late increase phase, but the expected peak in density in 1978 never occurred (Nyholm pers. comm.). In none of these years, the population density

approached that of a peak year and breeding was intense during both summers (Nyholm pers. comm.). Breeding data of the two colonies from northern Sweden were compared with those previously reported (Gustafsson et al. 1980) for a colony originating from a stable population in southern Sweden (Nyholm and Meurling 1979).

In the two North Swedish colonies, 1989 young (1001 in colony A and 988 in colony B) were born in 342 litters (170 and 172 respectively) from 56 (31 and 25 respectively) females.

Housing conditions as well as breeding routines were the same as for the South Swedish colony (Gustafsson et al. 1980). Breeding animals were kept in monogamous pairs in standard plastic laboratory mouse cages, measuring 40 × 20 × 15 cm, with wire mesh cover, wood cuttings for bedding and a commercial mouse food and water. Cages were cleaned and carrots were provided twice a week. The animals were kept in a photoperiod of 18L : 6D and at a temperature of 22 ± 5°C. Humidity was not regulated. Animals were usually paired when 60 to 180 d old, and kept as long as they reproduced successfully. Pairs were killed if the female was not visibly pregnant 50 d after delivery of the preceding litter. If the male died while the female still reproduced, a new male was supplied. Cages with pregnant females were checked daily for litters. Checking included weighing to rule out the possibility of litters being born and eaten without discovery. The day of discovery was designated day 0 of lactation and of the succeeding interbirth interval. Records were made of the number of young born and of the numbers of surviving young on days 0–6, day 10 and day 16. The number of young found on day 0 was used as litter size except in 64 cases (20% of the litters) where it was apparent from the weight loss of the female that one or more additional young had been born but completely eaten. In these cases, the number of young was estimated from the weight loss of the female by using the modal number of young born for that weight loss. Young were sexed, weighed, and individually marked by toe clipping on day 10 and weaned and weighed on day 16. Young voles were kept in groups of four or five animals of the same sex until pairing. To simplify comparison, previously published reproductive data (Gustafsson et al. 1980) from the South Swedish colony are included in tables and graphs.

3. Results

3.1. Body size

The North Swedish animals were heavier than the South Swedish ones. After delivery of the first litter, the weight (mean ± S.E.) of 28 North Swedish females was 23.8 ± 0.43 g and that of 36 South Swedish ones was 21.4 ± 0.36 g. Sexually mature North Swedish males were also heavier than South Swedish ones of similar

Tab. 1. Frequency distribution of litter size, and relation between survival of young and litter size in two North Swedish and one South Swedish laboratory colony of bank voles.

		1	2	3	4	5	6	7	8	9	10	11	12	13	Total
Colony A	No. of litters	1	2	13	19	35	38	33	18	8	2	1			170
	% of litters	0.6	1.2	7.6	11.2	20.6	22.4	19.4	10.6	4.7	1.2	0.6			100.1
	% survival	0	50.0	41.0	40.8	54.9	51.8	56.7	70.8	26.4	0	72.7			52.2
Colony B	No. of litters	3	9	14	15	36	34	24	25	10	1				172
	% of litters	1.7	5.2	8.1	8.7	20.9	19.8	14.0	14.5	5.8	0.6				99.9
	% survival	66.7	55.6	54.8	60.0	46.7	46.6	36.9	27.0	37.8	0			0	40.5
North Swedish (A + B)	No. of litters	4	11	27	34	71	72	57	43	18	3	1			342
	% of litters	1.2	3.2	7.9	9.9	20.8	21.1	16.7	12.6	5.3	0.9	0.3			100.2
	% survival	50.0	54.5	48.1	49.3	50.7	49.3	48.4	45.3	32.7	0	72.7		0	46.4
South Swedish	No. of litters	18	44	97	154	211	169	75	22	5	4				799
	% of litters	2.3	5.5	12.1	19.3	26.4	21.2	9.4	2.8	0.6	0.5				100.1
	% survival	38.9	60.2	69.4	75.7	81.1	77.9	76.4	74.4	40.0	60.0				76.2

age (23.9 ± 0.53 g, $n = 24$, versus 21.6 ± 0.35 g, $n = 38$). In both cases, the difference was significant ($t_{(62)} = 4.27$, $p < 0.001$ for females and $t_{(60)} = 3.75$, $p < 0.001$ for males). No differences between colonies A and B were seen.

3.2. Litter size

Litter size varied from 1 to 13 with a mode of 6 in the North Swedish colonies, and from 1 to 10, mode 5, in the South Swedish (Tab. 1). No difference between colonies A and B were seen. The litter size was dependent on the sequence of litters with smaller litters for primiparous females than for multiparous females (Fig. 1). In the North Swedish colonies, litter 1 was smaller than litters 3, 4, 6, and 7 (LSD procedure of multiple

comparisons, $p < 0.05$). This pattern was similar to that seen in the South Swedish colony, but litter size was larger in the North Swedish colonies than in the South Swedish one (two-way anova, effect of origin, $F_{(1,951)} = 42.1$, $p < 0.001$ and effect of order of litter, $F_{(9,951)} = 6.5$, $p < 0.001$. Only litters 1–10 were included).

The weight of the female after delivery was recorded in 106 cases in colonies A and B. A two-way anova of litter size versus order of litter and weight of the female revealed no significant effect of weight on litter size ($F_{(5,105)} = 1.105$).

3.3. Survival of young

Survival of young was significantly higher in colony A than in colony B, and significantly lower in both North Swedish colonies than in the South Swedish one (Tab. 1, χ^2 -test used for comparison). The pattern of mortality during the suckling period was similar in North Swedish and South Swedish animals, with most (83 and 70%, respectively) of the loss occurring during the first two days (Fig. 2).

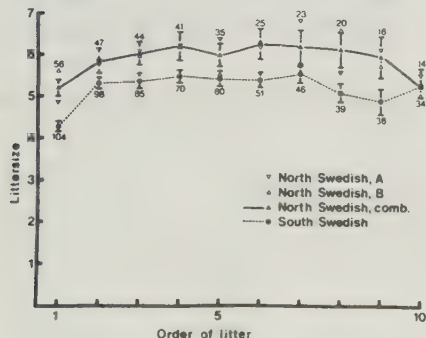


Fig. 1. Relation between order of litter and litter size in two laboratory colonies of bank voles of North Swedish and one of South Swedish origin. The number of observations is given for the South Swedish, and for the combined North Swedish colonies.

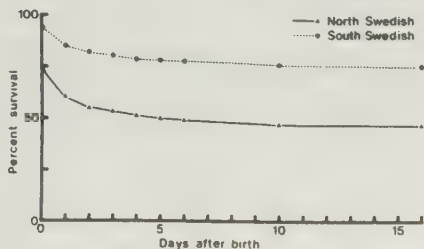


Fig. 2. Survival during the suckling period in young bank voles from two laboratory colonies of North Swedish and one colony of South Swedish origin.

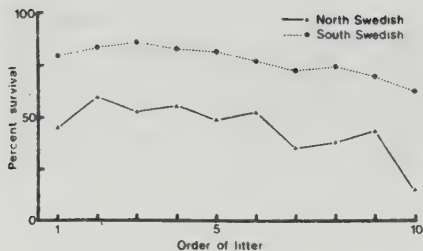


Fig. 3. Survival of young in relation to the order of litter in bank voles of North and South Swedish origin. The numbers of litters are the same as in Fig. 1.

In South Swedish animals, survival was higher in litters of medium size than in small or large litters. In colony A survival was highest in medium size litters, while it was highest in small litters in colony B (Tab. 1).

Like litter size, survival of young was influenced by order of litter, with lower survival in litter 1 than in litters 2 to 5–6 and again lower survival later in reproductive life (Fig. 3). After the tenth litter, survival continued to decrease in both North Swedish and South Swedish colonies.

3.4. Growth of young

The number of sucklings affected growth of young with maximal growth in litters with 2 or 3 sucklings. The North Swedish young grew faster than the South Swedish ones, and were significantly larger both when 10 and 16 d old (Tab. 2). Young from colony B were

significantly heavier than young from colony A when 10 d old, but not when 16 d old (two-way anova, weight versus colony and number of sucklings, effects of colony, $F_{(1,153)} = 4.2$, $p < 0.05$ at day 10 and $F_{(1,119)} = 2.3$, $p < 0.1$ at day 16).

3.5. Duration of pregnancy and interbirth interval

The duration of pregnancy was recorded for 25 primiparous North Swedish females. In all cases, young were born 18 d after observed mating. This duration of pregnancy was similar to that reported for South Swedish females.

The frequency distribution of interbirth intervals in the North Swedish animals was quite similar to that seen in the South Swedish ones, with a mode of 19 d for non-lactating and 22–23 d for lactating females and with 66% of the recorded intervals between 16 and 27 d long. Like in South Swedish animals a small second peak in the distribution of intervals in lactating females was found at days 36–40, indicating a lactational anoestrus. In South Swedish animals interbirth intervals shorter than 28 d were shown to result from post-partum matings. This was assumed to be the case also in North Swedish animals as the distribution of interbirth intervals was similar. Longer intervals excluded, the length of the interval was strongly affected by the number of sucklings (Fig. 4). The North Swedish animals had significantly longer interbirth intervals than the South Swedish ones (Fig. 4, two-way anova, effect of origin of animals, $F_{(1,731)} = 7.7$, $p < 0.01$, effect of number of sucklings $F_{(9,731)} = 33.4$, $p < 0.001$). The number of young alive on day 5 was used as the number of sucklings since delayed implantation is the cause for the prolonged intervals and because implantation takes

Tab. 2. Weight of young when 10 and 16 d old in relation to the number of sucklings in bank vole colonies of North and South Swedish origin.

10 d old					16 d old			
South Swedish			North Swedish		South Swedish		North Swedish	
No. of sucklings	No. of litters	Weight (g) Mean $\pm$ S.E.	No. of litters	Weight (g) Mean $\pm$ S.E.	No. of litters	Weight (g) Mean $\pm$ S.E.	No. of litters	Weight (g) Mean $\pm$ S.E.
1	16	5.31 $\pm$ 0.38	5	5.80 $\pm$ 0.58	16	7.56 $\pm$ 0.54	4	8.25 $\pm$ 0.63
2	49	5.96 $\pm$ 0.18	14	7.11 $\pm$ 0.44	51	8.47 $\pm$ 0.24	9	10.72 $\pm$ 0.62
3	76	6.16 $\pm$ 0.12	17	6.81 $\pm$ 0.16	82	8.74 $\pm$ 0.15	15	9.79 $\pm$ 0.37
4	112	6.04 $\pm$ 0.09	33	6.57 $\pm$ 0.17	122	8.60 $\pm$ 0.12	25	9.61 $\pm$ 0.30
5	131	5.80 $\pm$ 0.07	44	6.33 $\pm$ 0.11	150	8.46 $\pm$ 0.09	36	9.58 $\pm$ 0.21
6	87	5.57 $\pm$ 0.09	22	6.36 $\pm$ 0.21	99	8.19 $\pm$ 0.12	18	9.12 $\pm$ 0.25
7	33	5.62 $\pm$ 0.14	25	6.00 $\pm$ 0.18	36	8.44 $\pm$ 0.20	22	8.49 $\pm$ 0.21
8	5	4.89 $\pm$ 0.36	6	6.21 $\pm$ 0.23	6	6.89 $\pm$ 0.41	5	8.86 $\pm$ 0.48
9	1	4.25			1	6.71		
Total	510		166		563		134	
Mean		5.80		6.44		8.43		9.44

At both ages, the weight was significantly affected by the origin of the animals ($F_{(1,668)} = 52.9$, $p < 0.001$ at day 10 and $F_{(1,660)} = 62.7$, $p < 0.01$ at day 16) and by the number of sucklings ($F_{(8,668)} = 8.3$, $p < 0.001$ at day 10 and $F_{(8,668)} = 4.3$, $p < 0.001$ at day 16).

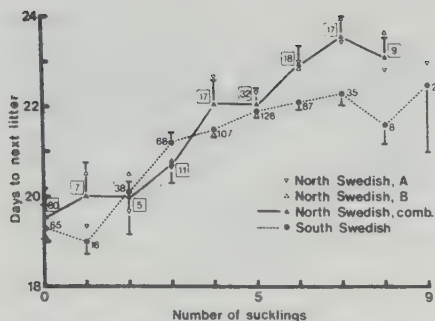


Fig. 4. Relation between the number of sucklings and the interval to the next litter in bank voles of North (2 colonies) and South (1 colony) Swedish origin. The number of observations is given for the South Swedish and the combined North Swedish colonies.

place at about day 5 in non-lactating females (Andersson and Gustafsson 1979).

3.6. Sex ratio

The sex ratio found in the North Swedish young was 220 males to 206 females in litters where all young survived, not significantly different from 1:1. When all litters were included the ratio was 502 males to 432 females, significantly more males than females ($\chi^2 = 5.24$, $p < 0.025$, young sexed when 10 d old). A predominance for males was found also in the South Swedish colony (and in a Polish colony, Buchalczyk 1970).

4. Discussion

The reproductive differences found between North and South Swedish bank voles are listed in Table 3. Other comparisons of reproduction between cyclic and non-cyclic populations of the same species of vole are few. In Scandinavia, only two field studies have been done: Stenseth et al. (unpubl.), where reproductive data for *C. glareolus* and *M. agrestis* from trappings over a long period in several areas in Sweden was treated, and Nyholm and Meurling (1979), where reproduction of *C. glareolus* in southern and northern Sweden was compared. In both studies reproduction in the cyclic population was suppressed, with, e.g. shorter breeding season and smaller litters at peak density than during the increase phase. Whatever the cause for this may be, we assume that there was no density dependent suppression of reproduction in our laboratory colonies. Therefore, the most valid comparison with field data is to compare our results with differences between stable

populations and cyclic populations during the increase phase. Reproductive data for two species of vole from such populations are summarized in Tab. 4. It shows that similar differences were found between South Swedish and increasing North Swedish populations of both species. Further, a comparison with Tab. 3 shows that differences found in field studies are very similar to those found in our laboratory. Only two differences can be seen: 1) *Litter size*. Stenseth et al. (unpubl.) reported larger litters in South Swedish young of the year than in North Swedish ones. This was found in both *C. glareolus* and *M. agrestis*. In the present study, size of the first litter was larger in North Swedish animals. This agrees with other field data for *C. glareolus* (Nyholm and Meurling 1979, Nyholm pers. comm.) where North Swedish young of the year had larger litters. The difference between the two field studies could be due to different methods of age estimation: Stenseth et al. (unpubl.) used pelage characteristics while Nyholm and Meurling (1979) used length of molar roots. The latter method is quite accurate (Gustafsson et al. 1982). Using pelage, in late summer spring-born young might be classified as overwintered. 2) *Weight at weaning*. While we report higher weight of newly weaned North Swedish young than of South Swedish ones, Stenseth et al. (unpubl.) found no difference between populations in weight of the youngest trappable animals. However, this kind of estimate is very difficult to obtain from field studies.

There are several possible explanations to differences in litter size between populations. Fleming and Rauscher (1978) suggested that the larger litter size in northern populations could be caused by a shift towards older animals. However, we found marked differences in litter size in animals of similar age but of different origin. In natural bank vole populations, litter size is affected by body weight (Zejda 1966), and if this could be applied to between-population differences, the larger North Swedish animals could be expected to have larger litters. A general association between body size and litter size in the bank vole is however contradicted by that the very large voles found on Skomer Island

Tab. 3. Differences in reproduction in captivity between bank voles of North Swedish (N) and South Swedish (S) origin. The magnitude of the differences are not given as in most cases the variables are also strongly dependent on other factors, impossible to include in a table.

Feature	Difference	Significance
Weight of adults, ♂	N>S	$p<0.001$
Weight of adults, ♀	N>S	$p<0.001$
Litter size	N>S	$p<0.001$
Litter size, first litter	N>S	$p<0.001$
Survival	N<S	$p<0.001$
Weight at weaning	N>S	$p<0.01$
Length of interbirth interval	N>S	$p<0.01$

Tab. 4 Reproduction in South Swedish (S) and increasing North Swedish (N) populations of *Clethrionomys glareolus* and *Microtus agrestis*. Data from (1) Stenseth et al. (unpubl.), (2) Nyholm and Mcurling (1979; data from trappings after 1976 courtesy of E. Nyholm) and (3) data courtesy of E. Nyholm.

Feature	Species	N	S	Difference	Signif. of difference	Notes	Source	
Weight of adults	♂	C.g.	25.7	23.8	N>S	S	June, overwintered	(3)
	♀	C.g.	29.0	25.0	N>S	S	June, overwintered	(3)
Litter size		C.g.	6.4	5.3	N>S	S	Overwintered, main breeding season (MBS)	(2)
		C.g.	5.6	5.2	N>S	S	Overwintered (MBS)	(1)
		C.g.	6.6	4.5	N>S	S	Young of the year, MBS	(2)
		C.g.	3.6	4.1	N<S	NS	Young of the year, MBS	(1)
		M.a.	6.4	5.3	N>S	S	Overwintered, MBS, optimal habitat	(1)
		M.a.	5.2	5.1	N>S	NS	Overwintered, MBS, suboptimal habitat	(1)
		M.a.	4.1	4.6	N<S	—	Young of the year, MBS, optimal habitat	(1)
		M.a.	3.4	4.5	N<S	—	Young of the year, MBS, suboptimal habitat	(1)
Weight of juveniles	C.g./M.a.			N=S			(1)	
Length of interbirth interval ¹		C.g.	21.39	19.98	N>S	S?	Overwintered, MBS	(2)
		M.a.	19.67	18.83	N>S	—	Overwintered, MBS, optimal habitat	(1)
		M.a.	20.63	18.95	N>S	—	Overwintered, MBS, suboptimal habitat	(1)

1. Computed from the percentage of visibly pregnant and lactating females.

have very small litters (Jewell 1966). In our colonies, no significant effect of body weight on litter size was found, but the number of observations was not very large. The tendency was towards larger litters in larger animals.

A likely cause for the high mortality of North Swedish young is the presence of the stud in the breeding cage. In a separate experiment, where ten primiparous North Swedish females were isolated after mating, mortality of young was very low. The reason why the presence of the stud increases mortality much more in North Swedish than in South Swedish voles may be that the North Swedish animals were much more active and ran about much more. A similar difference in activity between North and South Swedish animals was reported in field voles by Rasmuson et al. (1977). Apart from these differences reproduction in the two colonies was very similar and was affected in the same way by most factors. This was also confirmed by the fact that the interaction term was non-significant in all two-way anovas where North and South Swedish animals were compared.

Stenseth (1978) suggested that an animal's optimal life history depends on the degree of cyclicity of the population. Different reproductive characteristics are favoured in cyclic and stable populations, resulting in genetical differences between populations. Specifically, in uncrowded situations larger litters and shorter intervals between litters would be expected in cyclic than in non-cyclic populations. Our data are consistent with the first prediction but not with the second. A similar dif-

ference in litter size between cyclic and non-cyclic populations was reported by Tamarin (1977).

Stenseth (1978) also predicted that the ratio of litter size of overwintered females to litter size of yearlings should increase with increasing population cyclicity. Such a relation was reported by Stenseth and Framstad (1979). In the laboratory, a greater difference between the maximal litter size and that of primiparous females is expected in colonies from cyclic than from non-cyclic populations. Using data from Lackey (1978), Stenseth and Framstad (1979) found such a relation in two *Peromyscus leucopus* populations. In our data, the ratio of maximal litter size (in relation to order of litter, Fig. 1) to litter size of primiparous was, on the contrary, larger in the South Swedish (1.29) than in the North Swedish (1.20) population.

This work shows that laboratory experiments can be used to shed light on the regulation of reproduction in relation to cyclicity, as reproductive differences between natural populations are preserved in laboratory colonies. The differences are likely to be genetical and the results thus support the concept of selection for different reproductive variables in populations with different degrees of cyclicity.

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INFLUENCE OF THE SOCIAL ENVIRONMENT ON SEXUAL MATURATION

OF MALE BANK VOLES, *CLETHRIONOMYS GLAREOLUS*

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ABSTRACT

The social regulation of sexual maturation in male bank voles, *Clethrionomys glareolus*, originating from a noncyclic, South Swedish population, was studied. Males kept together with an adult male from weaning until 40 days old were similar, in terms of sexual as well as somatic development, to those kept singly. Cohabitation with an adult female resulted in a slightly delayed puberty.

In contrast to the small effects of caging young males with known adults, daily confrontations with unknown bank voles caused a marked suppression of sexual maturation. Suppression was seen in males confronted with unknown adult males or females as well as in those confronted with unknown juvenile males. The effect may be species specific; confrontations with female laboratory mice had no effect.

Daily addition of bedding, soiled by adult males, had no significant effect on puberty.

Although the animals were kept at room temperature, in a constant photoperiod, and on a constant diet, seasonal differences in the rate of maturation were seen. Males born in autumn - early winter developed slower, sexually as well as somatically, than those born in spring or early summer.

The findings indicate that the frequency of confrontations with unknown animals is one of the most important factors in regulating the rate of sexual maturation in bank voles. In natural populations, an increase in the number of confrontations with unknown individuals could be the result of an increase in the rate of migration, an increase in animal numbers, or both. The sex and state of maturity of the unknown animal appears to be of small importance. This implies that the total density rather than the number of reproductive adults is important in regulating maturation of at least male bank voles.

1.0 INTRODUCTION

Most Microtine populations have discrete breeding seasons, usually with summer breeding. In most species, young born in the early part of the breeding season are capable of maturing and breeding during the season of birth. Those born in the later part of the season seldom breed during that season. One important factor in determining the production of young in such populations is to what extent young of the year reach maturity and contribute to reproduction in the season of birth. In many populations this is dependent on population density. In low-density populations most young mature early, but at high density few or none reach maturity. This is seen in for example Clethrionomys glareolus (Wiger, 1979), C. rutilus (Koshkina and Korotkov, 1975), C. rufocanus (Kalela, 1957), Dicrostonyx groenlandicus and Lemmus trimucronatus (Krebs, 1964), Microtus townsendii (Beacham, 1980) and M. pennsylvanicus (Christian, 1971). This indicates that the social environment has a strong influence on the rate of sexual maturation.

The aim of the present series of experiment was to clarify which factors in the social environment are important in density dependent suppression of maturation in Clethrionomys glareolus.

Few laboratory experiments on density dependent regulation of sexual maturation in Microtines have been done. Lecyk (1967) reports a delay in sexual maturation in young male Microtus arvalis, grown up adjacent to cages with fighting adults. No effect was seen in females. Grouping of females at weaning suppresses maturation in M. pennsylvanicus (Pasley and McKinney 1973). Male Clethrionomys glareolus, originating from a cyclic population showed a delay in maturation when kept in groups of four, compared to isolated. No such effect was seen in males originating from a stable population. (Gustafsson, Andersson and Nyholm, 1983).

In female mice, puberty is affected by urinary pheromones. Pheromones produced by adult males accelerate puberty and pheromones produced by grouped females delay puberty (Vandenbergh, 1969; Drickamer, 1977, 1982). Presence of males accelerates maturation of females in several other species, for example Microtus ochrogaster (Hasler and Nalbandov, 1974). The situation in male mice is less clear, but males in groups suppress each other. This is seen both when adult males are present (Vandenbergh, 1971) and in groups of only young males (Jean-Faucher, Berger, de Turckheim, Veyssiere and Jean, 1981).

Density dependent suppression of maturation seems to be well developed in many species of the genus Peromyscus. In artificial populations of Peromyscus maniculatus, young born at high densities show reproductive inhibition (Terman, 1969). Also in P. maniculatus, males grown up in groups or with adult males are strongly inhibited compared to those raised in isolation or with females (Bediz and Whitsett, 1979). This effect is mediated by an urinary pheromone (Lawton and Whitsett, 1979). A similar inhibition of maturation was seen in P. leucopus, grown up below metabolism cages with populations of 8 - 14 animals (Rogers and Beauchamp, 1969).

The present experiments study the influence of 1. Presence of adults of either sex, 2. Exposure to unknown individuals, and 3. Exposure to urine from unknown males, on the sexual maturation of male bank voles. The animals studied came from a noncyclic population. There may be differences in the social regulation of maturation in cyclic and noncyclic populations (Gustafsson, Andersson and Nyholm, 1983).

2.0 MATERIAL AND METHODS

2.1 General Methods

Bank voles, Clethrionomys glareolus, from a laboratory colony kept at the Department of Zoology, University of Lund, Sweden, were used. The colony originated from a noncyclic population in southern Sweden. A description of colony management and reproduction has been published (Gustafsson, Andersson and Westlin, 1980). The experimental animals were kept in standard 40 by 30 by 20 cm plastic cages. Wood shavings were used as bedding, and the animals were fed a commercial mouse food, supplemented with rabbit food twice weekly. The photoperiod was 18L:6D.

The experiments were designed to study the effects of various social environments on the sexual maturation of males. Young males remained with both parents until weaning, and were then allotted to the different treatments. Experiment 1 was started with 16 day old males, all other experiments with 18 day old ones. The experimental animals were kept in the same room as the breeding colony. When 40 days old, the males were killed, and body weight and weight of testes, seminal vesicles and adrenals were recorded. In Experiment 1 preputial gland weight was also recorded.

2.2 Experiment 1

This experiment investigated the effects of the presence of adults on sexual maturation of males.

Three treatments were used:

- 1A Isolated.
- 1B With an adult female.
- 1C With an adult male.

Adults were at least 60 days old. When possible, groups of three littermate males, one for each treatment, were used. If only two males were available, they were allotted to two of the three treatments.

2.3 Experiments 2 - 4

These experiments investigated the effect of daily exposure to unknown animals. Young males were paired with other animals as above, but the other animal was changed daily. At least five "unknown animals" were used in circulation. Experiment 2 is a replication of one published earlier (Gustafsson and Andersson, 1981). A preliminary report on Experiments 2 and 3 has been published (Gustafsson, 1982).

The treatments were:

- 2A Isolated.
- 2B With an adult male.
- 2C With an adult male, which was changed daily.
- 3A With an adult female.
- 3B With an adult female, which was changed daily.
- 4A With a young (18-30 day old) male.
- 4B With a young male, which was changed daily.

In Experiment 2 groups of three littermate males, in the other experiments littermate pairs were used. When 30-32 days old, the young "stimulus" males in group 4A were changed to 18 day old ones.

2.4 Experiment 5

The intention was to investigate whether the effect of unknown animals seen in Exp. 2 - 4 was species specific. The design was as above, but the bank voles were subjected to familiar or unfamiliar laboratory mice.

The treatments were:

- 5A With an adult female laboratory mouse.
- 5B With an adult female mouse, which was changed daily.

As above, littermate pairs were used, and five or six mouse females were used in circulation.

2.5 Experiment 6

This was an attempt to investigate to what extent pheromones are involved in delay of maturation.

The treatments were:

- 6A Isolated.
- 6B Isolated, approximately 200 ml. of bedding soiled by males added daily.

The males used to obtain soiled bedding were adults, kept isolated. Each day, bedding was removed from three cages with adult males, mixed and distributed to the young males. At least nine adult males were used in circulation.

Table 1: Results of experiment 1. Body and organ weights of 40 day old male bank voles, grown up in different social environments. Pairs of treatments in the table consist of N littermate pairs, with one member in each treatment. Treatments: 1 A Isolated. 1 B With an adult female. 1 C With an adult male.

Treat- ment	N	Body, g		Testes, mg		Seminal vesicles, mg		Preputial glands, mg		Adrenals, mg	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
1 A	77	19.8 ^b	0.3	542.5 ^b	9.9	83.8 ^a	3.7	15.8	0.7	3.2	0.1
1 B	77	18.5 ^b	0.3	499.6 ^b	15.7	73.0 ^a	4.9	17.9	1.1	3.2	0.1
1 A	92	19.6	0.2	539.6	9.7	78.5	3.4	15.7	0.7	3.2	0.1
1 C	92	19.4	0.3	539.6	11.6	76.7	4.2	17.0	1.0	3.2	0.1
1 B	61	18.3	0.4	502.8	18.5	70.7	5.6	17.8	1.3	3.1	0.1
1 C	61	18.9	0.4	522.7	16.5	71.5	5.2	15.9	1.1	3.1	0.1

Wilcoxon's signed-ranks test was used for statistical comparisons. Means denoted with the same letter are significantly different, a: $P < 0.05$, b: $P < 0.01$.

Table 2: Distribution of preputial gland weights in 40 day old male bank voles, grown up in isolation (1A), with an adult female (1B) or with an adult male (1C).

Preputial gland, mg weight range	1 A per cent	1 B per cent	1 C per cent
1.0 - 5.0	2.9	7.6	9.9
5.1 - 10.0	11.8	19.5	12.1
10.1 - 15.0	32.3	15.2	25.2
15.1 - 20.0	35.3	17.4	22.0
20.1 - 25.0	12.5	13.0	16.5
25.1 - 30.0	2.2	12.0	7.7
> 30.0	2.9	15.2	6.6
n =	136	92	91

The distribution of groups 1A and 1B are different, $\chi^2 = 37.0$, $p < 0.01$, G-test of independence. The distribution of 1C is not significantly different from either 1A or 1B, $\chi^2 = 3.6$ and 9.1 respectively.

3.0 RESULTS

3.1 Experiment 1

Keeping a young male with an adult female caused a slight but significant decrease in body, testicular and seminal vesicle weights as compared to isolated. No effects on adrenal weights were seen (Table 1). In spite of their lower gonad and seminal vesicle weights, the males caged together with females appeared to have larger preputial glands than isolated. A closer look at the frequency distribution of gland size reveals a marked difference (Table 2). Isolated males had a more or less normal distribution of weights, whereas those kept together with females had a much larger number of very small and very large glands. Those housed with adult males had an intermediate distribution of preputial gland weights.

Table 3: Results of experiments 2 - 5. Effect of daily confrontations with unknown animals on puberty of male bank voles. Each experiment consists of N littermate groups, with one littermate male in each treatment. Treatments: 2 A Isolated. 2 B With an adult male. 2 C With an adult, changed daily. 3 A With an adult female. 3 B With an adult female, changed daily. 4 A With a juvenile male. 4 B With a juvenile male, changed daily. 5 A With a female laboratory mouse. 5 B With a female laboratory mouse, changed daily.

Treatment	N	Body, g		Testes, mg		Seminal vesicles, mg		Adrenals, mg	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
2 A	15	19.6 ^b	0.4	484.3 ^b	31.2	66.7 ^b	8.2	3.0 ^b	0.1
2 B	15	19.6 ^c	0.5	510.3 ^c	28.6	64.3 ^c	10.8	3.2 ^c	0.1
2 C	15	16.4 ^{bc}	0.5	320.6 ^{bc}	45.7	23.2 ^{bc}	8.1	3.9 ^{bc}	0.2
3 A	18	18.4 ^b	0.5	417.2 ^b	42.5	54.6 ^b	10.8	3.0 ^a	0.1
3 B	18	17.4 ^b	0.5	297.7 ^b	48.5	30.4 ^b	10.3	3.3 ^a	0.1
4 A	24	19.5 ^b	0.3	535.0 ^a	11.5	82.2 ^a	7.3	3.2	0.1
4 B	24	18.4 ^b	0.3	483.2 ^a	19.5	63.0 ^a	8.5	3.1	0.1
5 A	17	20.0	0.6	564.3	25.9	108.2	14.1	3.5	0.1
5 B	17	20.4	0.5	578.5	23.8	119.6	11.8	3.4	0.1

Only within experiment statistical comparisons were made. Means denoted with the same letter are significantly different, a: $p < 0.05$; b, c: $P < 0.01$, Wilcoxon's signed-ranks test.

3.2 Experiments 2 - 4

In all cases, exposure to unknown bank voles caused a marked delay of maturation compared with animals kept with one animal all the time (Table 3). Males kept with adult males or isolated did not differ. Those exposed daily to unknown males were strongly suppressed, compared with those isolated or permanently paired with the same adult male. Exposure to unknown adult females or young males also caused a strong inhibition of maturation. The adrenals were enlarged in groups 2C and 3B, but no effect on adrenal weight was seen in group 4B (Table 3).

3.3 Experiment 5

Exposure to unknown laboratory mice failed to cause any reproductive inhibition, nor did it affect adrenal weights (Table 3).

3.4 Experiment 6

Daily addition of bedding soiled by adult males did not significantly affect sexual maturation or adrenal weights (Table 4).

Table 4. Results of experiment 6. Effect of daily addition of male-soiled bedding on puberty of male bank voles. Body and organ weights of 40 day old males are shown. 38 littermate pairs of males, one member for each treatment, were used. Treatments: 6 A Isolated. 6 B Isolated, approximately 200 ml of male-soiled bedding was added daily. No significant differences were found.

Treatment	N	Body, g		Testes, mg		Seminal vesicles, mg		Adrenals, mg	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
6 A	38	20.0	0.4	516.4	17.5	79.2	6.8	3.2	0.1
6 B	38	19.6	0.3	500.8	20.3	68.1	6.6	3.1	0.1

3.5 Seasonal Variation

The experiments were run over several years, and although the conditions were kept as constant as possible, seasonal differences in the rate of sexual maturation were seen. Table 5 shows body and reproductive organ weights at 40 days of age in bank voles born in different months. Data from all experiments are included, but groups

2C, 3B, and 4B are excluded since they showed a marked inhibition of maturation. Groups 1A and 3A were included, in spite of the slight delay in maturation caused by adult females. Excluding them does not substantially alter the results. Males born in late summer, autumn and early winter show a delay in maturation compared to those born in spring. The seasonality also explains the difference in means between groups like 2A and B (animals from August - October), 3A (from August - January), 4A (from January - March) and 5A and B (from March - May). Experiments 1 and 6 contain animals from all months.

Table 5. Somatic and sexual development of 40 days old male bank voles in relation to month of birth. All animals were kept in 18L:6D at room temperature. Groups 1A-C, 2A, 3A, 4A, 5A-B and 6A-B are included. There is a significant effect of month of birth on body weight and organ weights. Results of analysis of variance: Body: $F(11,485) = 4.97$, $p < 0.001$, Testes: $F(11,485) = 6.16$, $p < 0.001$, Seminal vesicles: $F(11,485) = 7.24$, $p < 0.001$.

Month of birth	N	Body, g		Testes, mg		Seminal ve- sicles, mg	
		Mean	S.E.	Mean	S.E.	Mean	S.E.
1	52	19.2	0.4	546.5	17.7	81.7	6.4
2	46	19.5	0.4	533.8	13.2	74.0	5.1
3	57	19.1	0.3	548.1	10.7	95.2	5.4
4	50	20.0	0.3	538.8	14.1	92.0	6.2
5	24	21.0	0.5	597.2	15.8	110.4	7.9
6	30	19.8	0.4	558.4	16.8	91.2	7.9
7	29	20.1	0.4	556.3	17.4	92.5	7.3
8	54	19.8	0.3	522.2	14.7	78.9	5.1
9	41	19.9	0.5	522.0	19.6	70.7	6.9
10	61	18.5	0.3	456.9	17.6	52.0	4.8
11	26	19.2	0.6	496.6	29.4	76.5	8.9
12	27	17.3	0.5	417.0	29.5	47.2	7.1

4.0 DISCUSSION

Presence of a familiar adult had little effect on sexual maturation of young males. The effect seen, a slight delay in the rate of maturation in males kept with adult females, is unexpected. In some other species, for example mice (Vandenbergh, 1971) and Peromyscus maniculatus (Bediz and Whitsett 1979), males suppress other males, but there are to my knowledge no reports of nonsibling females suppressing males. The inhibiting effect of adult females may be related to the inhibition of maturation by presence of litter mates shown in M.

californicus and M. ochrogaster (Batzli, Getz and Hurley, 1977). In that experiment males and females kept with siblings were retarded, compared to those kept with nonsiblings. If sibling suppression occurs in Clethrionomys glareolus, it is possible that a male responds in the same way to a female introduced long before puberty as it would to a sibling female.

The effect of unknown bank voles on sexual maturation indicates that migration may be a very important factor in suppressing maturation in nature. In a sense, the frequency with which an animal meets unknown animals may be the best way for it to estimate density in a natural population. This could act on migrants as well as residents. If contact with unknown animals has a more general negative effect on reproduction, this could be part of the explanation for the early cessation of breeding seen in adults in some peak years (Kalela, 1957; Koshkina and Korotkov, 1975; Krebs, 1964).

Experiment 5 indicates that the effect seen has some species specificity, and is not merely an effect of frequent changes in the environment. One problem is however that the mouse females used were much less active than the bank voles, and may have been less effective for this reason.

Bedding soiled by unknown adult males apparently has little effect on male maturation. This is contrary to Peromyscus maniculatus, where daily addition of male-soiled bedding, or treatment with male urine, caused a strong inhibition of maturation (Lawton and Whitsett, 1979).

The effects on maturation, seen in these experiments, although marked, were far less dramatic than those seen in Clethrionomys glareolus originating from a cyclic population. Grouping of four young males caused a complete inhibition of puberty in many cyclic animals, whereas no effect whatsoever was seen in stable ones (Gustafsson, Andersson and Nyholm, 1983). In the present experiments, a much stronger stimulus (unknown animals) caused a much less marked delay of maturation. This may indicate that there are basic differences in sensitivity to social suppression of reproduction in animals from cyclic and stable populations.

The effects on the preputial glands call for a comment. The size of the glands is related to the social status. Males reared in isolation have small to medium-sized glands. When males are allowed to establish a dominance hierarchy, the preputial glands of the dominant male increase strongly in weight (Gustafsson, Andersson and Meurling, 1980). Thus, presence of another animal is necessary for developing large preputial glands. The most important hormone in regulating gland size is testosterone, the glands responding very rapidly to increased testosterone levels (Janet, 1978). This indicates that the animals with large preputial glands have higher testosterone levels. Possibly this would, in time, also result in larger accessory sexual organs.

The hormonal events in the suppression are unknown. Increased adrenocortical activity has been associated with reproductive inhibition in mice (Brain, 1971). ACTH inhibits maturation in Peromyscus leucopus (Pasley and Christian, 1972). The increase in adrenal weight in groups 2B and 3B may indicate stress involvement.

However, adrenal enlargement was not seen in group 4B despite this group being inhibited. Bank voles from a cyclic population showed reproductive inhibition when kept in groups of four, but showed no evidence of adrenal enlargement (Gustafsson, Andersson and Nyholm, 1983). Caution is needed in evaluating the adrenal weight data as adrenal weight is a poor measure of adrenocortical activity.

The seasonality seen in this study is similar to that reported in laboratory rats kept in a constant environment (Mock and Frankel, 1980). Other cases of seasonality in bank voles kept in a constant daylength and on a constant diet have been reported earlier. Young born in the period April to June showed better survival than those born at other times (Gustafsson, Andersson and Westlin, 1980). The cause for this seasonality is unknown, possibly the animals react to some subtle change in the environment, or they have some kind of internal annual rhythm in reproduction. It is not yet possible to make any statements about the relation of this seasonality to seasonality in a natural environment.

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Social environment and sexual maturation in male bank voles, *Clethrionomys glareolus* (Schreber, 1780)

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Introduction

In natural populations of many rodents the population density is important in determining the rate of sexual development of the young. In low density populations of many microtines, young born early in the reproductive season become sexually mature during the season of birth, whereas in dense populations few young reach sexual maturity during their first season. This has been described in for instance *Clethrionomys rufocanus* (KALELA 1957), *C. glareolus* (NYHOLM & MEURLING 1979), *Microtus pennsylvanicus* (CHRISTIAN 1971) and *Dicrostonyx groenlandicus* (KREBS 1964). The reason for this suppression of puberty is not clear. The cause may be social or be connected with food supply.

Few laboratory studies have been made on social suppression of puberty in small rodents. A negative effect of high density on sexual maturation in artificial populations has been described for mice (CHRISTIAN 1958). In *Peromyscus maniculatus* crowding resulted in inhibition of reproduction in young females (TERMAN 1965). On the other hand, *P. maniculatus*-females brought up in a group of 32 animals of both sexes per cage whereof four adults, had heavier gonads than males brought up with their parents, about eight animals per cage (THOMAS & TERMAN 1975). In mice a negative effect of adult males on the sexual maturation of young males has been described (VANDENBERGH 1971, MCKINNEY & DESJARDINS 1973). In *Microtus arvalis*, young males brought up in close proximity to cages with densely packed adults reached sexual maturity later than controls (LECYK 1967).

The present experiment was designed to study the effect of the presence of adult males on the sexual maturation in male bank voles, *Clethrionomys glareolus*.

Material and Methods

Male bank voles from a colony kept at the Department of Zoology, University of Lund, Sweden were used (see GUSTAFSSON, ANDERSSON & WESTLIN 1980). The voles were kept in standard plastic laboratory mouse cages (40x25x15 cm) with wire mesh lids and woodcuttings provided for bedding. Water and laboratory mouse pellets were always available, supplemented with fresh carrots twice a week. The photoperiod was 18L:6D.

Twenty-one males from seven litters, three males from each litter, were used. At weaning when 16 days old they were randomly assigned for one of three treatments:

A: Isolated B: In cohabitation with an adult male or C: Together with an adult male, which was changed every day. The adults used were at least three months old. In experiment C, the adult males were used in circulation so that the young males were not paired with one specific adult male more often than every third day. The young males were killed when 40 days old. Reproductive organs and adrenals were dissected out and weighed fresh. During the experiment the animals were kept in the same room as the breeding colony.

Results

Bodyweights and weights of reproductive organs and adrenals are given in Table 1. As no differences between litters could be seen, oneway analysis of variance was used to determine the effects of treatment on the different weights. No developmental differences between isolated young males and young males paired with an adult male were found. However, young males daily subjected to a new adult male showed retarded somatic as well as sexual

Table 1: Body weight, weight of reproductive organs and adrenals (mean $\pm$ S. E.) of young bank voles, in relation to the social environment.

Social environment	n	Body weight, g.	Testis weight, mg.	Sem. vesicles weight, mg.	Preputial glands weight, mg.	Adrenals weight, mg.	Relative adrenal weight mg/100 g bw
Isolated	7	20.5 $\pm$ 0.54	589 $\pm$ 28.2	101 $\pm$ 6.7	18.8 $\pm$ 3.30	3.0 $\pm$ 0.23	14.6 $\pm$ 1.06
With ad. ♂	7	20.7 $\pm$ 0.46	583 $\pm$ 19.2	107 $\pm$ 12.5	18.6 $\pm$ 2.34	3.3 $\pm$ 0.21	16.0 $\pm$ 1.06
Ad. ♂ changed daily	7	17.1 $\pm$ 0.64 ^b	370 $\pm$ 49.9 ^b	24 $\pm$ 15.7 ^b	8.3 $\pm$ 2.06 ^a	3.7 $\pm$ 0.42	22.5 $\pm$ 3.32 ^c

a, b: Different from both other groups, $p < 0.05$ and $p < 0.01$ respectively. Tukey method of multiple comparison (Afifi and Azen (1972)). c: Different from Isolated, $p < 0.05$.

development. Their relative, but not their absolute adrenal weight was higher than in both other treatment groups.

Discussion

The present study shows that the social environment can influence the sexual maturation in male bank voles, but the presence of one adult male during the maturation period is not a strong enough stimulus to cause any substantial retardation of development. The important stimulus in this case is the confrontation with a new adult male once daily. This experiment does not separate the effect of confrontation with unknown adult males from that of meeting unknown animals, irrespectively of their age and reproductive state. It seems valuable to conduct experiments to separate these effects.

The social inhibition of sexual maturation reported here may be related to the mechanism, which regulates puberty in natural populations. A young animal born in a dense population is more likely to be confronted with unknown animals than one born in a less dense population. This difference would be still more marked if, as suggested by CHRISTIAN (1970), migratory behaviour increases with increasing population density.

The higher relative adrenal weight in young males confronted with a new adult male daily may indicate increased adrenal activity. A suppression of gonadal development by the adrenals in these animals is therefore possible. Adrenals have been shown to increase in size in subordinate male mice (ARCHER 1970; BENTON, GOLDSMITH, GAMAL-EL-DIN, BRAIN & HUCKLEBRIDGE 1978) and in mice in dense populations (CHRISTIAN 1958, SOUTHWICK & BLAND 1959). The adrenal activity in such cases have been suggested as the cause for suppressed gonadal activity (BRAIN 1971; SUNG, BRADLEY & TERMAN 1977).

Summary

The social environment was found to influence sexual maturation in male bank voles, *CLETHRIONOMYS GLAREOLUS*. In young males which were subjected to a new adult male every day, sexual and somatic development was retarded compared to littermates which were isolated or in cohabitation with an adult male. The relative adrenal weight (mg/100 g bw) was higher in young males confronted with a new adult male daily.

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Comparison of sensitivity to social suppression of sexual maturation in captive male bank voles, *Clethrionomys glareolus*, Originating from populations with different degrees of cyclicity

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Gustafsson, T. O., Andersson, C. B. and Nyholm, N. E. I. 1983. Comparison of sensitivity to social suppression of sexual maturation in captive male bank voles, *Clethrionomys glareolus*, originating from populations with different degrees of cyclicity. – Oikos 41: 000–000.

Differences in sensitivity in male bank voles from three laboratory colonies, two established from a strongly cyclic population in northern Sweden and a third from an almost stable population in southern Sweden were investigated.

In males from the cyclic populations, sexual maturation was delayed in animals kept in groups of four per cage compared with animals kept singly or two per cage. No such differences were seen in males from the stable population. This difference in sensitivity to social inhibition of puberty is discussed with reference to a current hypothesis of evolution of different reproductive rates in populations with different degrees of cyclicity.

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Introduction

An important factor influencing reproduction in small rodent populations is the time of sexual maturation of the young. In many small rodent populations, sexual maturation is strongly influenced by population density. When density is low, most of the young mature early and a large part of the breeding population in the autumn consists of young of the year, whereas sexual maturation of young of the year is suppressed in years with high population density. This applies to several microtine rodents, such as *Lemmus trimucronatus* and *Dicrostonyx groenlandicus* (Krebs 1964), *Clethrionomys rufocanus* (Kalela 1957), *C. rutilus* (Koshkina and Korotov 1975) and *C. glareolus* (Nyholm and Meurling 1979).

The underlying mechanism of this suppression of maturation is unknown, but the cause is probably to be

sought in social stimuli. Social suppression of maturation has been demonstrated in several laboratory studies. In mice, the presence of an adult male delays sexual maturation of young males (Vandenbergh 1971) and in *Peromyscus maniculatus* grouping of young males or rearing of young males in the presence of an adult male suppresses maturation, while the presence of females has no such effect (Bediz and Whitsett 1979). Direct contact is not always necessary, since urine from adult males inhibits maturation of male *P. maniculatus* (Lawton and Whitsett 1979) and sexual maturation is delayed in young male *Microtus arvalis* reared near cages with fighting adults (Lecyk 1967).

In male *C. glareolus* of non-cyclic origin maturation can be inhibited by daily exposure to an unknown adult male, whereas the constant presence of an adult male has no suppressing effect (Gustafsson and Andersson 1980).

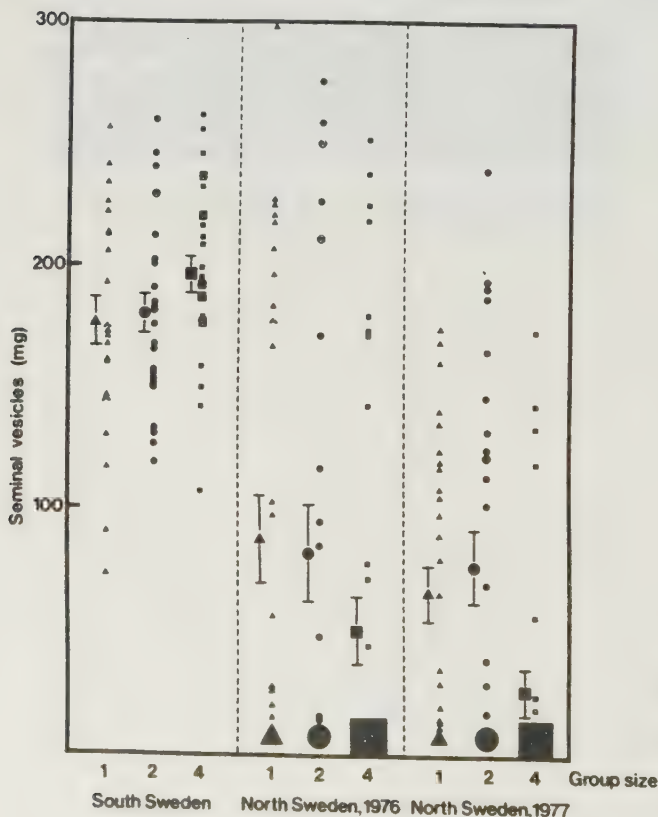


Fig. 1. Seminal vesicle weights in 60 d old male bank voles from South and North Swedish laboratory colonies as affected by group size. N is shown for dots representing more than one observation. For each colony and group size mean $\pm$ S.E. is also given.

The present study compares the effect of grouping on sexual maturation of male *C. glareolus* from three laboratory colonies, one originating from a non-cyclic, and two from a cyclic population.

Material and methods

The material consisted of 245 male bank voles, *Clethrionomys glareolus*, from three laboratory colonies, kept at the Dept of Zoology, Univ. of Lund, Sweden. Seventy males came from a laboratory colony established in 1974 with animals from South Sweden (Gustafsson et al. 1980) and 93 and 81 respectively from two colonies established in 1976 and 1977 with animals from North Sweden (Gustafsson et al. 1982). North Swedish populations are markedly cyclic, while South Swedish ones are almost stable (Stenseth et al. unpubl.).

The voles were kept in standard plastic laboratory mouse cages (40 × 20 × 15 cm), with wire mesh lids and with wood-shavings as litter. They were fed a commercial laboratory mouse food, and water. Twice a week the cages were cleaned and fresh carrots were supplied. The photoperiod was 18L : 6D.

At 16 d of age the animals from each colony were weaned and placed in separate cages with one (group I), two (group II) or four (group III) males in each cage and kept in the same room as the breeding colonies until sacrificed at 60 ± 3 d of age. The reproductive organs and adrenals were removed and weighed fresh.

Results

All South Swedish males were sexually well developed. All except two had seminal vesicles weighing over 100

mg (Fig. 1) and the lowest testicular weight was 392.6 mg. In contrast, inhibited males were found along with fully mature ones in all groups from the two North Swedish colonies. In 107 males the seminal vesicles weighed less than 50 mg (Fig. 1) and in 62 the testes weighed less than 100 mg. The South Swedish animals showed no social suppression of maturation in group III in comparison with group I (Tab. 1, Fig. 1). The only significant density dependent effect found was a higher testicular weight in group II, but the mean seminal vesicle weight was actually somewhat higher in group III than in either of the other groups.

In the two North Swedish colonies, the animals were not as sexually mature in group III as in the other two groups (Tab. 1, Fig. 1). In the males from the 1976 colony the only significant difference was in seminal vesicle weight, but when groups I and II were pooled, their testicular weight was higher than that in group III (Mann-Whitney U-test, $P < 0.05$, one-tailed). In the 1977 colony, the difference was more pronounced: in both group I and group II the animals were more developed, sexually as well as somatically, than those in group III.

No obvious density dependent effects on adrenal weights were seen (Tab. 1).

No comparisons of weights between North and South Swedish males were made. Fully mature North Swedish males raised in the laboratory are heavier than South Swedish ones (Gustafsson et al. 1982). The lower body weight in North Swedish males in this experiment is due to the strong correlation between sexual and somatic development (Tab. 1). Since it was not known whether the weights of reproductive organs and adrenals are similar in fully mature animals, direct comparisons seem unjustified.

Tab. 1. Body weight and weights of reproductive organs and adrenals in 60 d old male bank voles from South and North Swedish laboratory colonies as affected by group size. Weights are given as mean ± S.E. Group I = one male per cage, group II = two male per cage and group III = four males per cage.

Origin of animals	Group	n	Body wt (g)	Testes wt (mg)	Seminal vesicle wt (mg)	Adrenal wt (mg)
South Sweden	I	23	20.6±0.4	592.4±15.6 ^c	176.4± 9.8	3.8±0.2
	II	24	21.1±0.5	635.1±13.8	179.9± 8.1	3.7±0.1
	III	23 ^a	21.4±0.6	589.6±16.4 ^c	194.4± 7.7	3.5±0.1
North Sweden 1976 colony	I	30	18.3±0.5	358.2±51.7	88.3±17.9	4.5±0.1
	II	27	17.2±0.5	349.1±53.6	83.2±19.9	4.4±0.2
	III	36	17.2±0.4	260.1±47.6	51.2±14.0 ^b	4.2±0.1 ^b
North Sweden 1977 colony	I	27	19.3±0.5	421.7±46.3	67.1±11.6	4.3±0.2 ^c
	II	26	18.9±0.6	450.6±67.0	77.6±15.2	4.9±0.2
	III	28	17.3±0.4 ^{a,c}	210.1±43.7 ^{a,c}	26.2± 9.4 ^{a,c}	4.4±0.2

× One male with a testicular infection was excluded.

a. Different from group I, $P < 0.01$, Mann-Whitney U-test.

b. Different from group I, $P < 0.05$, Mann-Whitney U-test.

c. Different from group II, $P < 0.05$, Mann-Whitney U-test.

Discussion

The investigation showed that North Swedish male bank voles are more sensitive to social suppression of sexual maturation than South Swedish ones. However, the latter are not totally insensitive to the social environment since young South Swedish males exposed daily to an unknown adult male showed less development of reproductive organs than males kept singly or males kept constantly together with an adult male (Gustafsson and Andersson 1980).

Another difference between South and North Swedish small rodents in sensitivity to social stimulation has been demonstrated in field voles, *Microtus agrestis*, with similar differences in cyclicity (Nygren 1978). He found that although all voles reacted with increased locomotor activity to the presence of strangers, the response was much stronger in North Swedish animals than in South Swedish ones.

In addition to the density dependent effect on maturation, an overall difference between South and North Swedish animals was seen. Some immature animals were found in all North Swedish groups, whereas no such individuals were seen among the South Swedish ones. This difference may also be due to social inhibition of North Swedish males since the experiment was carried out in an animal room with approximately 300 bank voles. Since North Swedish animals are more affected by group size, they may also be more affected by smell or sounds from other animals. Olfactory stimuli have been shown to delay maturation in male deer mice, *Peromyscus maniculatus* (Lawton and Whitsett 1979), and presence of other animals in nearby cages delays maturation of *Microtus arvalis* (Lecyk 1967).

In our opinion, the difference in sensitivity of South and North Swedish males to social suppression of maturation in the present experiment probably reflects a similar difference in wild populations. This finds some support in field studies. Nyholm and Meurling (1979) found sexually mature young of the year in the increase year 1976, but not in the peak years 1973 and 1974 in a North Swedish population. In a South Swedish population, sexually mature young of the year were found in all the years from 1972 to 1976. In stable populations in Poland, young of the year comprised a large part of the breeding population in late summer in all years studied (Petrusewicz et al. 1971).

The difference in the rate of sexual maturation is also in agreement with Stenseth's hypothesis (1978), suggesting evolution of different reproductive strategies in populations with different degrees of cyclicity. He suggested that as density increases, the optimal strategy is to allocate fewer resources to current reproduction. A delay in maturation at high density has this effect. It is possible that the density of the South Swedish population is seldom so high as to favour lowering of the present rate of reproduction. If so, it would mean that evolution of a density dependent inhibition of maturation

would be favoured in populations reaching high densities (i.e. cyclic ones), but not in stable ones. The maximal density in the South Swedish population over a number of years was approximately a third of that found in a cyclic North Swedish population in the peak year of 1974 (Stenseth et al. unpubl.).

Another possible, although less likely, explanation for the difference found in this experiment, is that something in the laboratory environment affected the North Swedish animals adversely, and that already suppressed animals are more sensitive to social effects than unsuppressed ones. Possible adverse conditions are: 1) The North Swedish animals are more restrained by the cages than the South Swedish ones. North Swedish field voles (*Microtus agrestis*) are more active than South Swedish ones (Rasmuson et al. 1977). A similar difference was observed in our bank voles (unpubl. obs.). 2) In northern Sweden, the days are light for more than 18 h during most of the breeding season, and North Swedish animals may need a longer period of daylight than 18 h to develop normally. Further research is needed to clarify the underlying mechanism of the suppression of maturation.

A suppression of maturation in males probably has relatively little effect on the total reproduction in the population, since the number of overwintered males is presumably sufficient to fertilize reproducing females even if they young of the year are suppressed. On the other hand, a suppression of maturation of the females would have a much stronger effect on the total reproduction of a population. Preliminary observations indicate the existence of a similar difference in sensitivity to social suppression of maturation also in females.

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